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Strategic Environmental Research and Development Program
Conservation Thrust Area
(CS-758)

ECOLOGICAL MODELING TO SUPPORT LAND USE DECISIONS

FY 1997 Annual Report

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1. EXECUTIVE SUMMARY

The objective of this project is to provide DoD and DOE with ecological models that address issues in management of large land areas. During FY 1997, work was completed on evaluation of our habitat models for limestone glades/cedar barrens, Henslow's sparrow, and cerulean warbler. The territorial migrant bird model was modified to interface with the Integrated Dynamic Landscape Analysis and Modeling System at Fort Riley, Kansas. Work was begun on regional population dynamics models of red-cockaded woodpecker across the southern United States and of Karner blue butterfly at Fort McCoy, Wisconsin. One paper is in press and two have been submitted to open literature journals. Our SERDP work was presented at four national and international scientific meetings and at two national DoD conferences. Our work was discussed at several other scientific and DoD meetings. The products and approaches were also reviewed with land managers at three DoD installations. Our web site gives the current status of the effort (www.esd.ornl.gov/programs/SERDP).

2. BACKGROUND

Our modeling approach is based on a multiple-tiered system of models: vegetation dynamics models to predict structural changes in vegetation; habitat models that identify the presence and extent of habitat based on soils, vegetation, topography, geology, and other spatial attributes; local and regional population models that predict the trajectory over time of populations of species of conservation concern. All of these models are or can be spatially explicit, so that predictions can be related to specific features and areas on the ground. Our approach to modeling for this SERDP project is described in Dale et al. (in press).

Through FY 1996, project activities have concentrated on habitat models, local population models, and a vegetation dynamics model. Habitat models for limestone glades/cedar barrens, Henslow's sparrow (*Ammodramus henslowii*), and cerulean warbler (*Dendroicus cerulea*) were developed and tested at Fort Knox, though the evaluation of the test wasn't completed until FY 1997. A local population model for territorial migrant birds that was developed and applied specifically to Henslow's sparrows at Fort Knox, Kentucky. An existing vegetation dynamics model developed for western scrub vegetation was modified to incorporate the composition and structure of grassland and eastern deciduous forest vegetation.

3. FY 1997 ACTIVITIES

During FY 1997, our work expanded to larger regions and other DoD installations. Work was completed on evaluation of the field test of the habitat models. The limestone glades/cedar barrens habitat model, originally developed for Oak Ridge and tested at Fort Knox, was expanded to a regional scale and submitted for publication. The territorial migrant bird model was also completed and submitted for publication. Efforts on the vegetation dynamics model involved developing a basis for establishing initial conditions for the model. Two approaches for extrapolating patchy LCTA data to cover all of Fort Knox were tried. Work was begun on regional population models for the red-cockaded woodpecker (*Picoides borealis*) in the southern United States and the Karner blue butterfly (*Lycaeides melissa samuelis*) at Fort McCoy, Wisconsin. In order to facilitate communication of the utility of models to land management decisions, we developed a World Wide Web page (http://www.esd.ornl.gov/programs/SERDP/), which is organized around questions that arise in the course of managing natural resources. The following sections describe FY 1997 activities in each of these areas. A complete list of products developed in FY 1997 is included in Section 6.

3.1 Limestone Glades/Cedar Barrens Habitat Model

The limestone glade/barrens model is a regionally applicable model that predicts the occurrence and distribution of threatened limestone glade/barrens habitats both at the DoD installation and regional scales. Initial development of the model took place in 1994 on the Department of Energy Oak Ridge Reservation (DOE-ORR) where it accurately predicted six of the eight delineated cedar barrens/glade ecosystems management areas. The predictive ability of the model was then tested for a well-documented slope-glade complex at Fort Knox and was used to predict additional occurrences of open-glade habitat in active military training areas. Our model was more successful in predicting previously known areas at Fort Knox than on the ORR and accurately predicted all known sites within the Cedar Creek Slope Glades management area. In 1997, discussions with staff at Fort Knox indicated that the overall predicted glade ecosystem distribution for the remainder of Fort Knox was accurate. The total area of suitable substrate predicted by our model was about 970 ha, slightly more than the 890 ha estimated by Fort Knox natural resource managers. Subsequently, the soil component of the model was also applied to a multi-state region at a courser scale using the STATSGO regional soils data base. A manuscript describing the model, its application to Fort Knox, and the regional soil based application was submitted to a journal in September 1997. An overview of results were also presented as a poster at the annual Ecological Society of America meeting in Albuquerque, New Mexico, in August, 1997.

3.2 Field Test Of Habitat Models

During FY 1997, we completed evaluation of the field test of our habitat models at Fort Knox (see Appendix 2). Three conclusions can be drawn from the evaluation.

1. Despite inaccuracies in the land cover map available for Fort Knox, the habitat maps projected by the models were quite accurate. This analysis suggests that use of multiple GIS data layers and inductive training makes the models robust when compared to models based only on land cover. Underprediction could be reduced by using the product instead of the intersection of the deductive and inductive models.

2. Our limestone glades/cedar barrens habitat model predicts potential slope glades in a much broader area than that which has been already set aside for glade management. The Henslow's sparrow model predicts habitat for these birds in areas not currently identified as such by Fort Knox personnel. In both cases, field testing and discussions with field personnel suggests that the broader predictions are valid.

3. Although our models suggest a much broader areal extent of habitats, they also provide a means of focusing the field work required to verify the presence and status of these habitats. Thus, they offer a way to reduce the costs of future land management activities.

Habitat model results were provided to the ITAM coordinator and the wildlife biologists at Fort Knox and were consistent with their expectations abut distribution of the habitats. In addition, the results were presented in poster sessions at the SERDP Symposium in November 1996 and the ITAM Annual Workshop and Ecological Society of America meeting in August 1997.

3.3 Territorial Migrant Model

The territorial migrant model is an installation-scale model that addresses the demographics and persistence of migratory bird species that establish breeding territories on DoD installations. Initial development and implementation of the model took place in FY 1996. In FY 1997, the model was revised slightly and the model source code quality checked for accuracy and reliability. A manuscript describing the model and its application to Henslow's sparrow at Fort Knox, Kentucky was submitted for publication to Conservation Biology. The manuscript reviewed well, and is in revision for resubmission to Conservation Biology (see Appendix 3). A more general presentation of the model as "A model of spatially structured avian demographics" was given at the 1997 Annual Meeting of the International Society for Ecological Modeling, 4-6 August, Montreal, Quebec, Canada. The model was also parameterized and implemented for Henslow's sparrow at Fort Riley, Kansas, in coordination with the Argonne National Laboratory's Fort Riley application of IDLAMS (Integrated Dynamic Landscape Analysis and Modeling System).

3.4 Regional Population Model For Red-Cockaded Woodpecker

The red-cockaded woodpecker (RCW) model is a multi-installation model of regional RCW population dynamics across the species' entire geographical range. The RCW is a federally–listed endangered species, and populations of RCW occur on several DoD installations across the southern United States. Indeed, RCW populations on DoD installations are an integral and crucial component of the US Fish and Wildlife Service's (USFWS) Recovery Plan for RCW. These occurrences compel the need for DoD installation RCW management plans which are in accord with and contribute to the USFWS regional recovery plan.

During the first quarter of FY 1997 we investigated DoD needs with respect to RCW management in order to determine where the need for RCW modeling was the most acute, what type of models were needed, and where our modeling efforts might be most effective in forwarding the DoD's management of RCW. We reviewed published RCW literature, contacted RCW investigators about current activities, met with Tim Beaty at Fort Stewart in Georgia, consulted with USACERL, and consulted with Ralph Costa, head of the USFWS RCW Recovery Team. We determined that several installation-scale models were available with additional efforts underway, and that we could make the most effective contribution from a regional perspective that integrated DoD installation management with the USFWS regional recovery plan. We developed a regional RCW model in the 1st and 2nd quarters of FY 1997 and preliminary results of that model were presented at a national meeting (The 12th Annual Landscape Ecology Symposium, March 1997, Durham, NC) and a regional meeting (58th Annual Meeting of the Association of Southeastern Biologists, April 1997, Greenville, SC). Feedback from those presentations and from consultation with the USFWS RCW Recovery Team was positive. The remainder of FY 1997 was spent gathering the data from DoD installations and other Federal lands in the southern United States. These data are needed to refine the parameterization and implementation of the model. Results from this revised model are scheduled for presentation at the March 1998 meeting of the US Chapter of the International Association of Landscape Ecology.

3.5 Regional Population Model For Karner Blue Butterfly

The Karner blue butterfly (*Lycaeides melissa samuelis*) is a federally endangered butterfly whose distribution is restricted to the northern reaches of its host plant the wild blue lupine (*Lupinus perrenis*). Karner blue butterflies are abundant on Fort McCoy in Wisconsin and represent a potential constraint on land management and training at this installation. Being able to predict how management activities and training affect the distribution and abundance of the butterfly is important to informed ecosystem management.

Some researchers have suggested that the Karner blue butterfly may be distributed regionally as a metapopulation--a population structure where each individual subpopulation has a finite probability of becoming extirpated, but the entire species persists because of dispersal and recolonization among the various subpopulations. During FY 1997, we developed a preliminary

model of the Karner blue butterfly in order to examine the implications of assuming that individual subpopulations are linked by dispersal.

Our model assumes that the dynamics of each population follows a logistic growth function that can be modeled as a matrix of transition probabilities. Adults of one brood produce eggs at a given rate, a certain proportion of the eggs survive to become larvae, and a certain proportion of the larvae survive to adulthood. This three stage model is repeated for each of the two annual broods for each year that the model is run.

Subpopulations are defined spatially by the distribution of their habitat--primarily the presence of lupine. The dispersal capabilities of the butterfly (i.e., average dispersal distance) define the size of a subpopulation, and the probability of an individual butterfly to disperse long distances defines the dispersal between subpopulations.

Our preliminary model predicts the existence of three distinct subpopulations at Fort McCoy. This is consistent with the management plans of the installation.

3.6 Vegetation Dynamics Model

The vegetation dynamics model being developed involves a spatially explicit approach to predicting changes in vegetation cover and structure. Structure--i.e., the percent cover by life form (e.g., herbaceous plants, shrubs, deciduous trees, etc.)--is important to predicting the habitat for many wildlife species. For example, the Henslow's sparrow requires areas of clumped grasses with very little shrub or tree cover. Cerulean warblers, on the other hand, require large areas of old deciduous trees.

In order to predict vegetation changes on a spatially-explicit (i.e., pixel-by-pixel) basis, it is necessary to have a starting point for each pixel. These initial conditions should be derivable with data normally available to users of the model. One potential source of such data is the Land Condition Trend Analysis (LCTA) component of the Integrated Training Area Management (ITAM) program. However, LCTA data is available for only a relatively small number of plots (~140 at Fort Knox). Extrapolating from this small number of plots to all of Fort Knox was attempted in two ways. First, the land cover map developed in FY 1996 (in part from LCTA data) as part of the habitat modeling task was used to establish a land cover type for each pixel. The description of each land cover type in the LCTA data set was used to establish a value for the percent cover by each life form within that land cover type. This percent cover definition for a given land cover type was then applied to each pixel that was classified as having that land cover.

The second extrapolation approach involved geostatistics. In this approach, each LCTA plot represents a data point of known life form composition, and various geostatistical techniques (e.g., kriging) are used to infer the life form composition between LCTA plots.

These two methods of extrapolating LCTA data are likely to have value beyond vegetation dynamics modeling. An abstract has been submitted to present these LCTA data evaluation techniques at the 1998 ITAM meeting in Yakima, Washington.

4. BENEFITS OF APPROACH

Our approach to ecological models provides several benefits to natural resource managers by providing them with a method to identify locations of habitats at risk, a framework to analyze potential impacts of land use activities on natural resources, several case study demonstrations, and an approach that links management questions with models. Our approach is designed to be useful as well as useable. The models use information that is available to most installations. They can be adapted to similar concerns in other settings, and they provide outputs that reflect the concerns of land managers. These are characteristics of models that make them generally applicable to both site-specific and regional decisions.

5. FUTURE DIRECTIONS

5.1 Planned FY 1998 Activities

We will continue refinement of the regional model for the red-cockaded woodpecker across the southern states to provide a framework for evaluating the effectiveness of management efforts at individual DoD and DOE facilities. This model will also provide a valuable tool for reviewing draft revisions to the U.S. Fish and Wildlife Service's recovery plan for this species. Such revisions potentially affect management requirements at individual DoD and DOE installations.

The preliminary Karner blue butterfly model that was developed in FY 1997 will be expanded to include effects of changes in habitat quality on butterfly survival and to refine the assumptions and parameters used in development of the preliminary model. Improvements in the model will be coordinated with the IDLAMS team.

ORNL modelers will attend the Integrated Dynamic Landscape Analysis and Modeling System (IDLAMS) Modeling Integration Workshop. This technical workshop will focus on the status of IDLAMS and its relationship to the Army's Land Management System (LMS) and other DoD conservation activities. The role of ecological models being developed within this project will also be discussed.

As described in the original project proposal, we will quantitatively characterize land-use activities. A matrix of characteristics to describe land-use activities on DoD and DOE lands in terms of magnitude, frequency, areal extent, spatial distribution, predictability, and effects on habitat quality will be developed. Building on this matrix of characteristics, we will explore a land-cover change modeling approach.

Finally, building on our experience to date and incorporating input from DoD land managers, we will develop a final report that includes an evaluation of ecological modeling needs within DoD.

5.2 Beyond FY 1998

Although this project is currently scheduled to be complete at the end of FY 1998, we believe there are at least three areas where additional work beyond FY 1998 would be especially beneficial to SERDP and DoD. First is the area of communication between modelers and land managers. Models offer so much to the planning process but are so little used by land managers because of communication gaps. Land managers do not fully appreciate the potential of models, and modelers are often not aware of what information managers need. We believe that several actions can be taken to eliminate this gap between model potential and model use, but the key first step is to establish a formal dialog between modelers and managers.

Second, there is much yet to be done with regional population and habitat modeling. The approaches we are demonstrating for Karner blue butterfly and red-cockaded woodpecker can be expanded to other species of concern to DoD. Coupled with input from the dialog discussed above, regional models can become an important component of LMS and a highly useful tool for ecosystem management.

The third area of future effort is in collaboration with other DoD initiatives such as IDLAMS and LMS. Both of these programs provide a framework in which ecological models can be developed to address ecosystem management issues. Furthermore, ecological models that are useable by land managers are a critical component of LMS.

6. PAPERS, MEETINGS, AND PRESENTATIONS

6.1 Papers, Meetings, and Presentations Directly Supported by SERDP Funds

Papers

Dale, V. H., King, A. W., Mann, L. K., Washington-Allen, R. A., and McCord. R. A. In press. Assessing land-use impacts on natural resources. Environmental Management.

Submitted

King, A. W., L. K. Mann W. W. Hargrove, T. L. Ashwood, and V. H. Dale. 1997. Assessing the persistence of an avian population in a managed landscape: a case study with Henslow's sparrow at Fort Knox, Kentucky. Conservation Biology.

Mann, L. K., A. W. King, V. H. Dale, W. W. Hargrove, R. Washington-Allen, L. Pounds, T. L. Ashwood. Predicting limestone glade ecosystems in heterogeneous landscapes. Ecosystems.

Meetings

T. L. Ashwood. Third Annual Meeting of the Wildlife Society, Cincinnati, Ohio, October 1996.

T. L. Ashwood, V. H. Dale, and A. W. King: Coordination meeting, Fort Stewart, Georgia, January 1997.

T. L. Ashwood: 23RD ADPA Environmental Symposium, New Orleans, Louisiana, April 1997.

V. H. Dale: Workshop on Ecosystem Management, sponsored by the Strategic Environmental Research and Development Program, Arlington, Virginia, June 2-5, 1997.

T. L. Ashwood and L. K. Mann: Coordination meeting, Fort Knox, Kentucky, June 10,1997

T. L. Ashwood: Field survey and data reconnaissance, Fort McCoy, Wisconsin, August 5-7 1997.

V. H. Dale, A. W. King, and L. K. Mann: Ecological Society of America meeting in Albuquerque, New Mexico, August 10-14, 1997

T. L. Ashwood: MODSIM 97, Modeling and Simulation Workshop, Albuquerque, New Mexico, September 1997.

Presentations

King, A W., L. K. Mann, W. W. Hargrove, T. L. Ashwood, and V. H. Dale. A model of spatially structured avian demographics. Annual Meeting of the International Society for Ecological Modeling, 4--6 August 1997, Montreal, Quebec, Canada.

Dale, V. H. and T. L. Ashwood. Ecological modeling for military land-use decision support. SERDP Annual review, Arlington, Virginia, May 1997.

King, A. W., T. L. Ashwood, V. H. Dale, and L. K. Mann. Habitat fragmentation and regional persistence of the Red-cockaded Woodpecker. 12th Annual Landscape Ecology Symposium, 16--19 March 1997, Durham, NC.

King, A. W., T. L. Ashwood, V. H. Dale, and L. K. Mann. On the persistence of the red-cockaded woodpecker, *Picoides borealis*, in the southeastern United States. 58th Annual Meeting of the Association of Southeastern Biologists, 16--19 April 1997, Greenville, SC.

Posters

T. L. Ashwood and V. H. Dale, GIS-based habitat modeling at Fort Knox SERDP Symposium, Tyson's Corner, Virginia, November 1996.

L. K. Mann, V. H. Dale T. L. Ashwood . Predictive modeling of eastern limestone barrens in heterogeneous landscapes with multiple GIS data layers. Ecological Society of America meeting in Albuquerque, New Mexico, August 10-14, 1997

T. L. Ashwood, W. W. Hargrove, A. W. King, L. K. Mann, V. H. Dale and L. G. Pollack: Using LCTA data to build GIS-based habitat models at Fort Knox. ITAM Workshop, San Antonio, August 1997.

6.2 Related Ecological Modeling Products Not funded by SERDP

Papers

Stork, N. E., T. J. B. Boyle, V. Dale, H. Eeley, B. Finegan, M. Lawes, N. Manokaran, R. Prabhu, and J. Soberon. 1997. Criteria and indicators for assessing sustainability of forest management: conservation of biodiversity. Center for International Forestry Research Working Paper No. 17. Bogor, Indonesia.

Dale, V. H. In press. Managing forests as ecosystems: A success story or a challenge ahead? In (M. L. Pace and P.M. Groffman, editors). Successes, Limitations, and Frontiers in Ecosystem Ecology. New York: Springer Verlag..

Dale, V. H. 1997. Criteria and indicators for assessing sustainability of forest management: conservation of biodiversity. Bulletin of the Ecological Society of America 78:291-292.

Dale, V. H. and O'Neill, R. V. In Press. Tools for assessing environmental conditions, In (Dale, V. H. and English, M. R., editors) Tools for Environmental Decision-Making Research. New York, Springer -Verlag.

English, M. R., Dale, V. H., Van Riper-Geibig, C. and Ramsey, W. H. In Press. Tools to aid environmental decision making: an overview, In (Dale, V. H. and English, M. R., editors) Tools for Environmental Decision-Making Research. New York, Springer-Verlag.

Dale, V. H. and English, M. E. In Press. Next steps in designing and implementing analytic tools for decision making, In (Dale, V. H. and English, M. R., editors) Tools for Environmental Decision-Making Research. New York, Springer-Verlag.

With, K. A., and A. W. King. 1997. The use and misuse of neutral landscape models in ecology. Oikos 79:219--229.

King, A. W. 1997. Hierarchy theory: A guide to system structure for wildlife biologists. In J. A. Bissonette (ed.), Wildlife and Landscape Ecology: Effects and Patterns of Scale. Springer-Verlag, New York. (in press).

Submitted

With, K. A., and A. W. King. Extinction thresholds for species in fractal landscapes. Submitted to Conservation Biology.

With, K. A., and A. W. King. Dispersal success in fractal landscapes: a consequence of lacunarity thresholds. Submitted to Landscape Ecology.

Turner, M. G. and Dale, V. H. What have we learned from large, infrequent disturbances? Ecology.

Dale, V. H., Lugo, A. MacMahon, J. and Pickett, S. Management implications of large, infrequent disturbances. Ecology.

Presentations

T. L. Ashwood, R. A. Washington-Allen, B. E. Sample. Use of a GIS to assess risks to wildlife on a large federal facility. The Wildlife Society's Third Annual Meeting. Cincinnati, Ohio, October 2, 1996.

V. H. Dale: Workshop on "Tools to Aid Environmental Decision Making" sponsored by the NSF National Center for Environmental Decision Making Research, Knoxville, TN, Oct. 29-30, 1996.

V. H. Dale: NSF National Center for Ecological Analysis and Synthesis Symposium on "Synthesis in Ecology: Applications, Opportunities and Challenges," Santa Barbara, Cal., Nov. 18-20, 1996.

V. H. Dale: Cary Conference on "Use of Ecological Principles," Millbrook, New York, May 5-10, 1997

V. H. Dale: Ecological Society of America Symposium on "Advances in Spatial Modeling of Changes in Forest Landscapes," Albuquerque, New Mexico, August 10-14, 1997.

K. A. With and A. W. King. Uncritical thresholds in dispersal success on fractal landscapes. Paper presented at 12th Annual Landscape Ecology Symposium, 16--19 March 1997, Durham, NC.

K. A. With and A. W. King. 1997. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Abstract published in Bulletin of the Ecological Society of America} 78 (Supplement):331. Poster presented at the Annual Meeting of the Ecological Society of America, 10--14 August 1997, Albuquerque, NM.

Meetings

V. H. Dale: Workshop on "Criteria and Indicators for Monitoring Biodiversity", Bogar, Indonesia, April 21-25, 1997.

V. H. Dale: Workshop on Information Infrastructure for environmental decision making, Gatlinburg, TN., April 29-30, 1997.

PREDICTING LIMESTONE GLADE ECOSYSTEMS IN HETEROGENEOUS LANDSCAPES

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ABSTRACT

Soil is formed from the interaction of vegetation, climate, and parent material over long time periods. We used these characteristics of soil forming processes to develop a GIS model of limestone glade ecosystems on the Department of Energy Oak Ridge Reservation (DOE-ORR). The predictive ability of the model was then tested at the Department of Defense Fort Knox Military Reservation, Kentucky. The model predicts the presence of glade ecosystems from the combination of 1) soil taxon as an indication of moisture regime, vegetation history, and soil chemistry; 2) geology; 3) slope; and 4) satellite imagery to indicate successional state. The soil component of the model was also applied to a multistate region at a courser scale using the STATSGO regional soils data base. Lithic Mollisols (Rendolls and Udolls) and lithic Alfisols (Udalfs) were demonstrated to be associated with limestone glade ecosystems. This combined soil/geology/GIS approach has potential for highly accurate prediction of rare ecosystems with narrow edaphic constraints useful in long-term planning for conservation management. GIS analysis can help in conservation planning by quantifying habitat extent, identifying sites most suitable for restoration, and analyzing spatial relationships among sites, including potential dispersal patterns.

Keywords: <limestone glades> <barrens> <GIS> <Department of Defense> <Department of Energy> <conservation> <Mollisol> <soil taxonomy>

INTRODUCTION

Spatial characteristics of landscapes influence biodiversity (Fahrig and Merriam 1985, Kareiva 1990, Franklin 1993), sustainability (Lubchenco et al. 1991), and ecosystem management (Wear et al. 1996). These landscape characteristics, including soil physical and chemical properties, also influence and are influenced by ecosystem processes (Turner et al. 1995). Turner et al. (1995) argue for better understanding of links between ecosystem processes and landscape patterns in order to fully incorporate influences on biodiversity that are necessary for effective conservation management. The feedbacks between vegetation and soil characteristics have been fundamental to soil classification systems from the beginning, and spatial aspects of classification of soils are reflected in the concepts of soil associations and catenas (USDA-SCS 1975, Jenny 1980). Current soil surveys use aerial photography, land-use patterns, vegetation, and topography as cues to the spatial distribution of soil types, but the relationship between soil formation, disturbance history, and biodiversity has not been explored extensively at the landscape scale using current GIS technology (Ludwig and Tongway 1995, Davidson 1995). Soil forming processes used in classification of soils (e.g., moisture regime, influences of vegetation, and geochemistry) can provide a framework for predicting ecosystems narrowly constrained by edaphic features such as shallow soils over singular geologic formations. In this paper, we use the relationship between soil forming processes and landscape pattern to predict the occurrence of limestone glade ecosystems from data at different scales.

These limestone glade ecosystems occur throughout the eastern United States and have unique soil nutrients, water regime, and land-use history, as well as species composition (Quarterman et al. 1993). They occur in a landscape complex of bare rock, herbaceous vegetation, and xeric woodland, and adequate knowledge of their distribution and dynamics is not currently available (Dale et al. *in press*, Thomas 1996). They are of research and conservation interest because of 1) their rarity, 2) their importance as habitat for several globally and regionally rare endemic plant species, and 3) their potential to provide habitat for rare invertebrates and other wildlife (Noss et al. 1995). Like many other increasingly rare ecosystems, some occur on large, non-park public lands with primary use other than conservation such as military training and research, where access and traditional survey techniques may not be possible (Kentucky State Nature Preserves Commission 1994a, TNC 1995, Mann et al. 1996).

Using a Geographic Information System (GIS) has been widely accepted for describing spatial characteristics of landscape processes related to conservation of biodiversity (e.g., Scott et al. 1993, Jennings 1995, Barrio et al. 1997, Dale et al. *in press*). Models using a GIS have the potential to accurately predict locations of rare ecosystems in heterogeneous or inaccessible terrain with a minimum of field work (Lowell and Astroth 1989, Lauver and Whistler 1993, Sperduto and Congalton 1996, Dale et al. *in press*). Using known glade ecosystem characteristics of soil geochemistry, water regime, and vegetation successional state, we developed a GIS-based model to predict the occurrence of limestone glade ecosystems on the Department of Energy Oak Ridge Reservation (DOE-ORR) (Dale et al. *in press*). In this paper we further discuss the conceptual basis of our predictive model, focussing on the use of soil forming processes reflected

in the U. S. Soil Taxonomy (USDA-SCS 1975). We then evaluate a test application of the model at the Fort Knox Military Reservation, Kentucky. By working at two sites where the distribution of limestone glade ecosystems is only partially known, we were able to test the wider applicability of our model. Results of the model application include documenting comparable soil and geologic characteristics and resulting moisture regimes, similarities of occurrence of species that are of conservation interest, overall similarities in vascular plant species composition, and comparable successional states. Species of conservation concern at both sites are discussed in the context of glade ecosystem distribution, and species dispersal and persistence characteristics. We also applied the soil component of the model to a coarser scale, multistate region using the STATSGO regional soil data base (NRCS 1994) as a further test of the model's applicability, and include discussion of endemic vascular plant species distribution. We conclude that this approach can accurately predict the spatial distribution of rare ecosystems and species of conservation concern that have narrow edaphic constraints. This capability should be useful in conservation management.

LIMESTONE GLADE ECOSYSTEMS

In the eastern United States, where the dominant natural vegetation is forest, the term glade or barren has been used to denote natural, drought prone, open areas or areas where disturbances such as fire or grazing regularly removes tree species (Quarterman et al. 1993). Such forest openings often occur on shallow, rocky soils, including limestones of the southeastern U. S. In the literature about limestone openings, there is considerable overlap and contradiction in usage of the terms "barren" and "glade" with more recent usage consistently referring to glades and barrens as having perennial, warm season grass cover of <50% and >50 %, respectively (Quarterman et al. 1993, DeSelm and Murdock 1993). However, many limestone "glades" occur along a moisture gradient from extremely droughty bare rock and gravel glades, to deeper soils of barrens or prairies, to rocky, open woodland where deeper pockets of soil and cracks in rocks providing a more reliable supply of moisture (Quarterman et al. 1993). Gravelly sites of weathered limestone rock and accumulated soil and intermediate moisture regime are variously called cedar barrens (DeSelm et al. 1969, DeSelm 1993), xeric limestone prairie (Baskin et al. 1994), limestone barrens (TNC 1995), or limestone slope glades (White et al. 1994). Xeric woodland of eastern red cedar (*Juniperus virginiana)*, several species of oaks (*Quercus* sp.), and pines (*Pinus* sp.) form the matrix for glade openings. In this paper, we use "limestone glade ecosystems" to include the landscape complex containing the moisture and light gradients from open, rocky glades to the xeric woodland matrix.

Disturbance is an important factor in the persistence of small glade openings that may otherwise be shaded by encroaching woodland. In the absence of disturbance, patches of greater soil depth and cracks in the limestone provide enough moisture to allow gradual development of woodland canopy. Thus fire or other disturbance that removes the tree canopy is favorable (Lowell and Astroth 1989), but intensive grazing or summer mowing of herbaceous vegetation has resulted in species impoverishment of up to 65% (DeSelm 1989, DeSelm et al. 1969). Because of the importance of disturbance regimes in historical development of glade ecosystems and accompanying effects on soil formation, our conceptual definition of those systems includes a

temporal component. We hypothesize that herbaceous glade and barren vegetation has expanded into surrounding woodlands or contracted around central core areas of bare rock or gravel glade in response to changes in climate or disturbance regimes. Thus, our definition of limestone glade ecosystems includes surrounding xeric woodlands where existing soil formation indicates previous long-term presence of herbaceous vegetation. Although we do not explicitly examine such disturbance regimes, we do consider their influence on soil formation.

The flora of limestone glade ecosystems has been documented extensively (Quarterman 1950, Baskin and Baskin 1985, Baskin and Baskin 1986, Quarterman et al. 1993, DeSelm 1993). Glades of the Central Basin of Tennessee and northern Alabama often include areas of limestone rock that are large and level enough to allow water to pool temporarily during wet winter months, thus providing habitat for rare endemic species such as *Leavenworthia* spp. (Quarterman et al. 1993). These Central Basin glades contain the highest density and greatest number of rare endemic species of all the southeastern glades (Quarterman et al. 1993). Quarterman et al. (1993) and Baskin and Baskin (1986) consider glade vegetation west of the Mississippi to be more closely allied to prairie than glades east of the Mississippi. However, our soil-based model includes all potential glade ecosystems of the southeastern U. S. and assumes that limestone glade ecosystems in this region have developed in response to similar edaphic conditions.

THE STUDY SITES

Department of Defense (DoD) and Department of Energy (DOE) reservations are areas where increasingly rare habitats have been protected from urbanization and other land conversion for more than 50 years, often contrasting with surrounding development (Mann et al. 1996, Vogel 1997). The Nature Conservancy has identified the Cedar Creek Glades area of the Fort Knox Military Reservation, Fort Knox, Kentucky, as a significant conservation area, and the Oak Ridge Reservation (ORR), Oak Ridge, Tennessee, contains several registered State Natural Areas that contain limestone glade endemics (White et al. 1994, Pounds et al. 1993).

The Oak Ridge Reservation (ORR) consists of the Oak Ridge National Environmental Research Park and the DOE facilities at Oak Ridge, Tennessee, and covers about 15,000 ha of mostly contiguous native forest in Roane and Anderson Counties in the Ridge and Valley physiographic region (Figure 1). Prior to government acquisition in 1942 as a security buffer for military activities, the ORR's approximately 1000 individual farmsteads consisted of forest, woodlots, open grazed woodlands, and fields (Mann et al. 1996, Dale et al. 1990). In 1994, about 70% of the ORR was mostly oak-hickory (*Quercus-Carya*), pine-hardwood (*Pinus*-hardwood), or pine forest cover (Mann et al. 1996, Washington-Allen and Ashwood 1996). Less than 3,000 ha are buffer zones around developed sites for the three DOE facilities and less than 1,400 ha are waste sites or remediation areas.

Ecosystems with uncommon biota, often including globally rare species, occur within the mixed hardwood and pine forest matrix on the ORR and have recently been documented by The Nature Conservancy (Pounds et al. 1993, TNC 1995). The glade ecosystems of the ORR have often been referred to as "cedar barrens" because of the abundance of eastern-red cedar in the encroaching xeric woodland matrix and the presence of soil deep enough for dominance of perennial warm season grasses (DeSelm et al. 1969, Mann and Kitchings 1982, DeSelm and

Murdock 1993). These ecosystems contain several threatened and endangered endemic vascular plant species on the ORR and the adjacent Boeing Tract (historically part of the ORR) (Table 1).

Geology of the ORR is complex (Hatcher et al. 1992). Parallel ridges and valleys run southwest to northeast, with alternating limestone, sandstone, or shale and siltstone geology. The topography is a result of interstratified weak (valley) and erosion resistant (ridge) layers faulted and folded by at least two major thrust faults. Chickamauga limestone, associated with glade ecosystems throughout the Ridge and Valley (DeSelm 1993), occurs in two major valleys of the ORR as relatively linear features. There are narrow bands of several limestone formations in the Chickamauga group, including Lebanon, Moccasin, Witten, Bowen, Benbolt, Rockdell, Fleanor, and Lincolnshire. Because of their origin, these rock strata tend to be tilted and relatively narrow and linear in contrast to those in the Central Basin.

Documented limestone glade ecosystems on the ORR are characterized by: 1) less than about 5 % exposed, relatively unweathered limestone; 2) extensive areas of bare, shaley soil comparable to gravel glades of the Central Basin (estimated to be less than about 30 %); and 3) a highly diverse assemblage of grasses and forbs. These ecosystems are a heterogeneous mixture of glade (<50% perennial warm season grass cover), barren (>50% perennial warm season grass cover) (DeSelm and Murdock 1993, Quarterman et al. 1993), and xeric eastern red-cedar/mixed deciduous woodland, occurring primarily on slopes less than 25 %.

The other study site, the Fort Knox Military Reservation at Fort Knox, occupies 44,150 ha in Bullitt, Hardin, and Meade Counties in north central Kentucky (Figure 1). Bordered on the north by the Ohio River, the Fort Knox Reservation is divided by Muldraugh's Hill, a steep escarpment of the Highland Rim to the west and south of the Salt River. Northeast of the Salt River is hilly and forested and a karst plateau of rolling uplands and sinkholes is to the west (White et al. 1994).

Most of Fort Knox is forested, with young to mature mesophytic forest in ravines and sheltered slopes, bottomland hardwoods on floodplains of major rivers and streams, and xeric oak/pine/eastern red cedar woodlands on dry ridgetops and shallow soils, especially in the south. About 19,000 ha is in commercial forest. Non-forested areas include the munitions testing part of the 21,000 ha ordnance impact area in the center of Fort Knox and tank or tracked vehicle training areas on the karst plateau in the western and in the southeastern areas.

Limestone formations at Fort Knox are primarily of Upper Mississippian age. Some formations, such as the Ste. Genevieve and St. Louis limestones, that are usually under deeply weathered red clay (McDowell 1986) can be at the surface in erosional areas such as in the vicinity of the Cedar Creek Slope Glades (White et al. 1994). Salem and Harrodsburg formations weather to flaggy, gravelly surface soil similar in appearance and physical characteristics to that found on the Chickamauga limestone of the ORR and gravel glades of the Central Basin (McDowell 1986). All four of these geologic layers surface in the dissected region of the escarpment in the area of the glades.

Recent surveys by The Nature Conservancy and Kentucky State Nature Preserves Commission have identified several important conservation areas at Fort Knox, including the Cedar Creek Glades, which may be one of the highest quality examples of limestone glades in Kentucky (White et al. 1994) and contains several rare species (Table 1). Only the part of Fort Knox outside the training impact zone has been surveyed to identify locations of glade openings.

However, the glade ecosystem is known to be relatively extensive in the southern part of the reservation (White et al. 1994) and contains a mixture of highly disturbed and eroded areas resulting from vehicle use and logging operations, grazing, and fire. Gullies are present in steep areas adjacent to glades. The Cedar Creek Slope Glades preserve contains a small, relatively intact part of these glades in the southernmost part of the reservation. Grasses and components of prairie of the Midwest are characteristic (White et al. 1994).

METHODS

A combination of field experience with the ORR (Dale et al. *in press*, DeSelm et al. 1969, Mann and Kitchings 1982, Pounds et al. 1993, Cunningham et al. 1993, Mann et al. 1996) and existing literature concerning the Ridge and Valley and the Central Basin (Quarterman et al. 1993, Baskin and Baskin 1986, DeSelm 1993) is the basis of the model. The model combines distribution of substrate with a satellite "snapshot" of the disturbance regime and uses soil, geologic, and land cover characteristics that we expect to be predictive of glade ecosystems.

The soil component of our model capitalizes on soil forming processes underlying the current soil classification and taxonomy in the United States as used in soil surveys (USDA-SCS 1975). The taxonomy is hierarchical, with higher levels of the hierarchy related to soil forming processes resulting from interactions of vegetation, age, and relative topographic position. Comparable modifiers across lower levels of the hierarchy are related to temperature and moisture regime, depth to parent rock, and drainage. Diagnostic characteristics include the development of distinctive layers or horizons in response to vegetation influences on organic matter and geochemistry and to movement of water through the soil profile. The lowest level of the hierarchy is the soil series, which is often further subdivided into phases such as slope class or amount of erosion. In this taxonomic system, Mollisols are fertile, neutral soils, with a relatively homogeneous, highly organic layer near the surface. This organic layer is thought to have formed from an accumulation of organic residues in the presence of divalent cations, especially calcium, often under grass or herbaceous vegetation, such as in mid-western U. S. prairies. We hypothesize that at least some part of the areas currently occupied by glade ecosystems have been essentially without forest cover for enough time that soil development reflects the long-term presence of herbaceous vegetation cover and calcareous material such that Mollisols are present. Mollisols are atypical in humid, high rainfall regions under forest vegetation, but the Udoll suborder of soils (freely drained Mollisols of humid continental climates in mid-latitudes) and the Rendoll suborder (Mollisols of mostly forested regions that have formed from highly calcareous parent materials) could develop in glade ecosystems. We also speculate that Alfisols would be part of glade ecosystems, being intermediate in soil formation between Mollisols and other more typical soils of the southeastern U. S. Alfisols have developed less organic matter than Mollisols and generally have moderate base content. Entisols, soils without diagnostic horizons that have formed on very severely eroded slopes stripped of diagnostic surface soil, might also be a minor component.

No soil exists on bare rock - soil surveys usually map such rocky areas in complex or as inclusions in other map units. If mapped as a separate soil type, these soils are usually classed at a lower level of the soil taxonomic hierarchy as lithic soils, defined as less than 50-cm to solid rock

(USDA-SCS 1975). We restricted our model to soils of this class in order to use the widely available soil taxonomic information contained in soil surveys for our prediction, although some pockets of deeper soil would be expected to occur (Quarterman et al. 1993).

The geologic component of our model assumes that calcareous limestone bedrock is present. Furthermore, the limestone is assumed to occur as thin- to medium-bedding planes separated by calcareous shale that weather into the typical 'flags' or small bits of flat, gravelly rock. This rock is characteristic of "cedar barrens" on the ORR and the gravel glades of the Central Basin. The limestone rock is either at the surface or is covered with shallow soil, and it contributes to high pH, high calcium content, and poor water holding capacity of the soil. Lebanon limestone of the Chickamauga group is the typical substrate in the relatively flat glades of the Central Basin in middle Tennessee (Quarterman et al. 1993). Limestone of the Chickamauga group also occurs in the Ridge and Valley, but these areas are erosional surfaces that were exposed following faulting and folding in contrast to the large areas of flat rock in the Central Basin.

We used satellite imagery to generate data layers of Anderson Level I and II land cover classes (Table 2) (Anderson et al. 1976). We also assumed that glade ecosystems would be associated with certain land cover classes and not associated with others, such as mature oak-hickory forest. These land cover classes are "snapshot" surrogates for disturbance history. Land cover categories of "urban", which mimics bare rock, and "transitional", representing open eastern red-cedar-hardwood woodlands, as well as barren and grassland categories were positive filters for the presence of glade ecosystems. Because species of conservation concern occur predominantly occur in glade openings and not in the forested matrix, we excluded areas of closed canopy forest.

GIS data layers of soil, geology, slope, and land cover were input for the model. Data for the ORR and Fort Knox sites are from a variety of sources (Table 2) (Dale et al. *in press*) and regional soils data are from the STATSGO data base (NRCS 1994).

Sources of floristic data for Oak Ridge were Mann and Shugart (1983) and previously unpublished ORR species lists. Species lists for the ORR include data from Crowder Cemetery State Natural Area and surrounding glade ecosystems on the Boeing tract, the Oak Ridge Barrens within the city of Oak Ridge, and three areas on the ORR: McCoy Branch Embayment Barren and Walker Branch Embayment Barren Natural Areas and Raccoon Creek Barren Research Park Reference Area. White et al. (1994) was the source of data for Fort Knox. Our lists of glade species for both Fort Knox and the ORR include all species found in the complex of known glade and xeric woodland matrix sites, which yielded a larger assemblage of species than would have occurred in any one small glade opening. Sørenson's index of similarity (100% x number of species common to both sites ÷ [1/2 {total glade species at ORR + total glade species at Fort Knox}]) (Mueller-Dombois and Ellenberg 1974) was calculated for comparison of the ORR and Fort Knox glade ecosystem flora. Floristic data for the regional application of the model and comparisons of Fort Knox, ORR, and the Central Basin of Tennessee were Baskin and Baskin (1986) and Somers et al. (1986).

The accuracy of our prediction of occurrence of limestone glade ecosystems on the ORR was assessed by intersecting the predicted locations with a GIS layer of the administrative boundaries of the ORR's seven documented habitats for rare glade species and one potential

location (Pounds et al. 1993, Dale et al. *in press*). The model was considered successful if the administrative boundary contained a patch of predicted glade ecosystem. The model was then applied to Fort Knox and tested using a similar approach. At Fort Knox, glade openings are narrowly delineated within one large administrative boundary, the Cedar Creek Glades. Therefore, the model was considered successful if the delineated boundaries of glade openings either contained or were part of a predicted patch. As a further test of the soil component of the model, the STATSGO regional soil data base was used to predict general distribution of glade ecosystems in the eastern United States. For this test, only mesic or thermic lithic Mollisols (Rendolls and Udolls) were included. We selected soil landscape associations that contained one or more series that were lithic Mollisols that occur on limestone substrate, contained flat limestone fragments, indicating thin-bedded limestone parent material, and had a neutral or alkaline pH. This approach necessitated reviewing soil series descriptions to determine parent material and landscape associations of minor soils not included in the association name. Results were evaluated by comparing county level distribution of known glade endemic species (Baskin and Baskin 1986). Percent success of the model was determined from the co-occurrence of predicted glade ecosystems and endemic species.

RESULTS AND DISCUSSION

In Dale et al. (*in press*), we reported the correct prediction of six of the eight locations of delineated cedar barrens/glade ecosystems on the ORR (see Figure 1). Additional predicted habitat outside of administrative boundaries includes previously undocumented limestone glades, roads and rights-of-way through limestone glade areas, and areas of lithic Alfisols on the Fleanor and Lincolnshire formations of the Chickamauga limestone that do not support characteristic glade species. Recent erosion has been severe in some of these areas. Lithic Mollisols on the ORR were Rendolls and Argiudolls and lithic Alfisols were Hapludalfs (Table 3).

Our model was more successful in predicting previously known areas at Fort Knox than on the ORR and accurately predicted all known sites within the Cedar Creek Slope Glades boundary (Figure 2). Greater accuracy may have been due to differences in map data sources, in disturbance history, or in delineation of glade ecosystem boundaries. Several areas not previously documented as glades were predicted at Fort Knox. The total area of suitable substrate predicted by our model was about 970 ha, slightly more than the 890 ha estimated by Fort Knox Natural resource managers (Fort Knox 1995).

Although Baskin et al. (1994) and White et al. (1994) previously reported Ste. Genevieve and St. Louis limestone as substrate for glades in Kentucky, these limestones did not fit the required physical characteristics of our model. Our model successfully used Salem and Harrodsburg limestone (Table 3), and we found that Salem limestone was associated with all known openings of the Cedar Creek Slope Glades shown in Figure 2. Unlike the ORR, Mollisols at Fort Knox were mapped as Argiudolls (Corydon series) -- no Rendolls were mapped (Arms et al. 1979, Whitaker and Waters 1986) (Table 3) perhaps indicating a longer history without tree cover at Fort Knox. Only 15 ha of rock outcrop complex containing lithic Mollisols were present at Fort Knox, or less than 2% of the total. Garmon soil (a dystric Eutrochrept) is reported by Baskin et al. (1994) as the primary soil on which xeric limestone prairies occur in Hardin and

LaRue Counties in the Fort Knox area. However, the Hardin County Soil Survey includes thin bands of Hapludalf Caneyville-Rock outcrop complex (Arms et al. 1979) within the Garmon soil map unit that are probably the correct soil type.

Discussions with staff at Fort Knox indicate that the overall predicted glade ecosystem distribution appears to be accurate, but also includes areas of exposed, deeper soil in tank training areas that would revert to woodlands if left undisturbed. Hagerstown soil is associated with the open cedar hardwood woodland matrix in which the glade openings occur and is part of the ecosystem of conservation concern (White et al. 1994). Although areas mapped as Hagerstown soil contain small areas of shallower Caneyville soil (Arms et al. 1979), none of the known glade openings occurred on this soil type (Figure 2) and it is probably primarily woodland unless trees are removed by disturbance. These deeper soils may have been part of more extensive openings in glade ecosystems during extensive drought such as the dry warm period between 9000 and 4000 years B. P. (Delcourt et al. 1986).

In the regional application of the model using the STATSGO database, soils are delineated at the association level with resolution of 1 km pixels. Even in this coarse scale comparison, our soil model is coincident with the location of 99 of 158 county occurrences of glade endemics (Figure 3). The counties with known occurrences that were not predicted by our model may not have current county soil survey data (i.e., some of the Ridge and Valley counties in Tennessee) or soil map units are too small to detect at this scale (Nettleton et al. 1996). Some may be mapped as Alfisols or other soil types not considered in this application of our model. Some of the overprediction of area of glades in the Ozarks is due to broad mapping of some soil types in this region (e.g., Gasconade series), including different landforms and substrates, whereas glades in this region more commonly occur on west facing slopes (Lowell and Astroth 1989).

The ability of our ORR model to accurately predict the location of glade ecosystems at Fort Knox and throughout the eastern United States at a coarse scale implies a fundamental similarity between the "cedar barrens" of the ORR and the "slope glades" of Fort Knox. This similarity is also reflected in the vascular plant species common to the sites. Fifty-six herbaceous and five tree species are found in both the Fort Knox and ORR limestone glade ecosystems with a Sørenson's index of similarity of 30%. This is a greater similarity than reported by DeSelm et al. (1969) among several barrens and glades in east Tennessee, though less than similarities among middle Tennessee glades reported by Bridges and Orzell (1986). Of greater conservation interest, nine of 33 species that were the most frequent taxa of Central Basin glades (Somers et al. 1986) were common to both sites (Table 1). *Hypericum dolabriforme* was the only species found at both sites which is restricted to limestone glade openings in the eastern United States, but six protected species are known to occur on the ORR or Fort Knox (Table 1) (Pounds et al. 1993, King et al. 1994, White et al. 1994).

Conservation of threatened and endangered species in glade ecosystems requires attention to species distribution, persistence, and dispersal characteristics as well as predicting substrate location. A mixture of endemic, western prairie, and widely adapted weedy species is characteristic of glade ecosystems and includes many state and globally rare species (Table 1) (Baskin and Baskin 1986). Of the species occurring at Fort Knox and the ORR glade ecosystems, the state rare species *Liatris cylindracea, Solidago ptarmicoides,* and *Spiranthes magnicamporum* are primarily western species where they are more common. Many of these

species are well adapted to rapid expansion from woodland areas into recent disturbances. Of the 46 native species at both Fort Knox and the ORR, more than 38 are characteristically found in both open woodlands and openings, indicating an ability to persist in woodlands with at least partially closed canopy (Fernald 1970, Somers et al. 1986, Quarterman et al. 1993). Terletzky and Vanauken (1996) also report one third of glade species of the Edwards Plateau were found in both woodlands and openings. This apparent tolerance for a range of canopy coverage and its attendant effects on light levels, moisture, nutrients, and organic matter, indicates adaptation to disturbance and may also indicate an ability to exploit a suite of microsites that increase the probability of germination in variable climate. Thomas (1996) found year to year variation in weather affected survivorship of seedlings of a Missouri glade annual in shaded versus open microsites. As Thomas states, habitat heterogeneity may be important to the long-term persistence of these species in the harsh and unpredictable environment of glade ecosystems.

Most glade ecosystem species are either annuals with abundant seed production and fast germination or wind or wildlife dispersed perennials that can rapidly re-invade new openings (Table 1). For example, on the ORR, we observed that *Silphium terebinthinaceum*, a good indicator species of limestone glade ecosystems, quickly invaded disturbed areas underlain by Chickamauga limestone following establishment of pine plantations, especially in areas where soil was shallow to bedrock. In this case, the cedar hardwood woodland matrix was partially replaced by *Pinus taeda* and bare soil provided opportunity for *Silphium* populations to expand. On the Boeing tract of the ORR, several years use as a maneuvering ground for military tanks by the national guard provided an intermittent disturbance regime compatible with persistence of Tennessee state endangered *Liatris cylindracea*, *Solidago ptarmicoides,* and *Agalinus auriculata.* In a survey of species importance values on the Boeing tract, *Liatris cylindracea,* state Threatened in Kentucky and also present at Fort Knox, was found to have an importance percentage greater than 5 % (Table 4), indicating tolerance to this type of disturbance. Intensive tank training would probably be destructive to populations of these species, but periodic less intensive use of the area at Oak Ridge resulted in minor soil disturbance and removal of small invading trees. In another area, a population of *Delphinium exaltatum* expanded rapidly on a newly created 90-m-wide utility corridor and is abundant in older utility corridors managed by annual winter mowing after seed capsule maturation (Mann et al. 1996). Removal of tree cover by fire also allows expansion of rapidly colonizing species (Lowell and Astroth 1989, White et al. 1994). Conversely, many limestone glade ecosystems outside of relatively protected areas such as the DOE and DoD reservations are impoverished from intensive human use such as agriculture and urbanization. Our model only incorporates disturbance at one moment in time by using current land cover, but maintaining the endemic flora of glade ecosystems requires more detailed understanding of disturbance regimes and population dynamics.

Quarterman et al. (1993) noted that glades that are outliers to the central basin glades are "somewhat depauperate in endemics and in characteristic species, with many of these sites showing gradations from glade to barren". Species whose seeds are dispersed mainly by gravity such as *Lesquerella* spp. (Table 1) are particularly poorly adapted to crossing gaps more than 100 m wide (Primack and Miao 1992). Very small, light seeds, such as those of *Hypericum dolabriforme,* and wind dispersed seeds, such as those of *Liatris cylindracea,* could potentially be moved farther distances in windy periods (Howe and Smallwood 1982), but might not move

beyond intervening woodlands. Long, narrow areas of habitat have been predicted to have a higher likelihood of local plant population extinctions than rounder areas due to lower seed sowing densities or greater matrix-edge effects (Pounds 1995). If distances between patches of suitable habitat are greater than the ability to disperse between patches and if individuals or seeds are unable to persist over time under a relatively closed woodland canopy in the absence of disturbance, local population extinction probabilities are greater. Permanent loss of habitat to urbanization and other intensive land uses has the potential to exceed the capacity of some of the rarer and currently localized populations to persist in the landscape.

Detailed analysis of metapopulation dynamics of glade species is beyond the scope of this analysis. However, we present a preliminary comparison of species/area relationships in Figure 4, which integrates our results from the model with the occurrence of most frequent endemic species characteristic of Central Basin glade ecosystems. Accurate estimates of total area in lithic Mollisols of the Central Basin and the ORR were not readily available, but from the Anderson County Soil Survey (Arms et al. 1979), we estimate that the total area of lithic Mollisols on the ORR is at least 10 times greater than the estimated total of 15 ha at Fort Knox. Similarly, from soil association maps in Tennessee (Springer and Elder 1980), we estimate lithic Mollisols in the Central Basin occupy at least 10 times more area than on the ORR. These "core" areas of lithic Mollisols correlate roughly with the number of endemic species present (Figure 4), and raise questions about the relationship between available ecosystem patch size and persistence or establishment of metapopulations of endemic species. Are, for example, the more regularly distributed glade ecosystems of the Ridge and Valley more prone and sensitive to fragmentation than the irregular dispersed glade substrate at Fort Knox? Is total available area more important and are populations relatively insensitive to the pattern of patches? The more aggregated pattern of glades in the Central Basin and, at a much smaller scale, at Fort Knox contrast with the linear pattern of glades in the Ridge and Valley, where narrow valleys are somewhat isolated by intervening ridges (Dale et al. *in press*). These patterns suggest the potential for differing population extinction rates or rare species as a result of fragmentation.

Two ecosystem processes affect persistence of glade ecosystems - spatial distribution of suitable substrate and temporal changes in light availability related to disturbance (canopy removal). Terrestrial ecosystems are generally classified according to the species composition of the dominant vegetation and associated climate, often ignoring substrate (TNC 1994). Temporal changes can also be minimized by characterizing ecosystems at such a fine scale that dynamic interaction of species across changing successional stages within the landscape may be overlooked. For instance, a stand of mature southern pine (*Pinus virginiana* and *P. echinata*) forest that develops in an opening in an oak-hickory (*Quercus - Carya)* forest is part of the same watershed, with dynamic exchange of nutrients, water, and organisms, but the stand may be variously defined as part of an oak-pine ecosystem, or as a pine ecosystem, depending on the scale of observation. A more dynamic interpretation of ecosystems encompasses successional stages that form complex associations of contrasting vegetation types. Identifying our study sites as limestone glade ecosystems avoids some of the confusion generated by using separate names (e.g., glades, grassy glades, cedar glades, cedar barrens, or xeric limestone prairie) for various combinations of bare rock, perennial warm season grass dominated sites, herb dominated sites, and xeric woodlands. By including marginal woodland habitat outside of the glade opening, this

definition should improve analyses of metapopulation characteristics of organisms in patchy habitats, especially where habitats and organisms are threatened or endangered (Wahlberg et al. 1996).

CONCLUSIONS

We have developed a method for predicting the occurrence of limestone glade ecosystems using GIS application of known environmental requirements that incorporates past effects of disturbance history on soil formation. On the ORR and at Fort Knox, model results confirmed that Mollisols were associated with part of the glade ecosystem, indicating that at least portions of these sites may have been dominated by herbaceous vegetation for some time. At both locations, additional areas known to be part of the glade ecosystem were located on soils not classed as Mollisols. The fact that these areas of soil were usually Alfisols, supports our hypothesis that these areas have a mixed history of vegetation cover. Before intensive urbanization and intensive agricultural use, core areas containing both grassy barrens and rocky glades may have acted as centers of dispersal for limestone glade species with increasing or decreasing surrounding open areas in response to disturbance from fire, large herbivores, and drought cycles. These core areas would develop soils currently mapped as lithic Mollisols. Although county level soil surveys often map unusual habitats in complex with or as inclusions within other soil units, especially where small areas of shallow, rocky soil occurs, combining remote imagery and other data layers with soil data works well to identify limestone glade ecosystems.

This approach of defining ecosystems on the basis of soils and other spatial information should be effective for ecosystems that have strong edaphic constraints. In old growth forest, native grasslands, or other ecosystems in which successional characteristics or differences in disturbance history are more important constraints than moisture gradients or substrate characteristics, additional data coverage on land-use history is needed to attain similar accuracy. Many species are adapted to survival, reproduction, and recolonization in these highly fragmented and episodically disturbed limestone glade landscapes. Combining substrate, gap crossing ability, and spatial data can help in planning management of glade ecosystems and in conservation of rare species.

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Tables

Figures

Table 1. Characteristics of glade ecosystem vascular plants in the southeastern United States.

Species	Longevity	Seed dispersal characteristics[1]	Likely dispersal mode	ORR	Ft. Knox	Legal status[2]	
						Federal	State
Agalinus auriculata	annual	reticulated, small	wind/water	X		S	TN-E
Astragalus tennesseensis	perennial	none, small	gravity				TN - T
Allium cernuum[3]	perennial	bulbs, small	gravity	X	X		
Arenaria patula[3]	perennial	small	gravity/wind	X			
Aristida longespica[3]	annual	bristles, large	gravity/animal				
Carex crawei[3]	perennial	resin dotted, large	gravity/animal				TN-S, KY-S
Croton capitatus[3]	annual	flattened, lumpy, large	gravity				
C. monanthogynus[3]	annual	large	gravity	X	X		
Dalea foliosa	perennial	indehiscent pod, large	water, gravity			E	TN-E
Dalea gattingeri[3]	perennial	winged, large	water/gravity				
Delphinium alabamicum	perennial	large	water, gravity				
Delphinium exaltatum	perennial	ridged, large	water/gravity	X			TN-E
Diodia teres[3]	annual	toothed, large	gravity/animal	X			
Echinacea tennesseensis	perennial	ridged, large	water/gravity/ animal			E	TN-E
Erigeron strigosus[3]	annual? e	pappus, large	wind/animal	X			
Euphorbia dentata[3]	annual	lumpy, large	gravity	X			
Hedyotis nigricans[3]	perennial	small	gravity/wind	X			
Heliotropium tenellum[3]	annual? e	large	gravity		X		
Hypericum dolabriforme	perennial	small	gravity/wind	X	X		
H. sphaerocarpum[3]	perennial	small	gravity/wind	X	X		
Isanthus brachiatus[3]	annual	large	gravity	X			
Leavenworthia alabamica	annual	winged, large	gravity				
L. crassa vars.	annual	winged, large	gravity				
L. exigua vars[3]	annual	winged, large	gravity			S	TN-T & E, KY-T
L. stylosa[3]	annual	winged, large	gravity				
L. torulosa	annual	winged, large	gravity				TN-T, KY-T
L. uniflora	annual	winged, large	gravity				
Lesquerella lyrata	annual	inflated silicles, large	water				
Liatris cylindracea	perennial	pappus, large	wind	X	X		TN-E, KY-T

Lobelia appendiculata var. gattingeri	perennial	small	wind/water				KY-E
Manfreda virginica[3]	perennial	fleshy, large	gravity/animal	X	X		
Nothoscorodum bivalve[3]	perennial	bulbs, large	gravity				
Onosmodium molle subspp.	perennial	pitted, large	gravity				TN-E, KY-E
Oxalis priceae	perennial	explosive, large	gravity				KY-H
Panicum capillare[3]	annual	tumbleweed, large	wind/gravity/ animal	X			
Panicum flexile[3]	annual	large	gravity/animal	X			
Penstemon tenuiflorus	perennial	small	gravity				
Phacelia dubia	annual	reticulate or pitted	gravity				
Psoralea subacaulis[3]	perennial	large	gravity				
Psoralea stipulatum	perennial	large	gravity				
Rudbeckia triloba[3]	annual/biennial	large	gravity/animal				
Ruellia humilis[3]	perennial	small	gravity	X	X		
Satureja glabella[3]	perennial	reticulate, large	gravity				
Schizachyrium scoparium[3]	perennial	hairs, large	wind/animal	X	X		
Scutellaria parvula[3]	perennial	bumpy, large	gravity	X			
Sedum pulchellum[3]	annual	small	gravity/wind	X			
Senecio anonymus[3]	? perennial	hairs, large	wind	X			
Silphium terebinthinaceum	perennial	toothed, large	gravity/animal	X	X		
S. laciniatum	perennial	toothed, large	gravity/animal		X		TN-T, KY-T
Solidago gattingeri	perennial	pappus, large	wind/animal				TN-E
Solidago ptarmicoides	perennial	pappus, large	wind/animal	X			TN-E
Solidago shortii	perennial	pappus, large	wind/animal			E	KY-E
Spiranthes magnicamporum[3]	perennial	small	wind/gravity		X		KY-T
Sporobolus vaginiflorus[3]	annual	large	gravity/animal	X	X		
Talinum calcaricum[3]	perennial	rough, large	gravity				TN-T, KY-E
Verbena simplex[3]	perennial	reticulate, large	gravity	X	X		
Viola egglestonii	perennial	eliasome, large	ants, gravity	—	X		KY-S

[1] From Baskin and Baskin (1988) and references cited therein, or derived from Fernald (1970), Gleason (1952), or unpublished data for similar genera. Small < 0.5 mm, large >0.5 mm.

[2] E= Endangered; T = Threatened; S = Special concern; H = historic records, presumed extirpated.

[3] Characteristic, most frequent limestone glade endemics of the Central Basin, Tennessee (Somers et al. 1986).

Table 2. Summary of spatial data used to characterize glade ecosystems.

Theme	ORR	Fort Knox
Land cover - Anderson level I and II land use/land cover categories (Anderson et al. 1976)	1994 Landsat Thematic Mapper (TM) quarter scene raster from EOSAT corporation (Washington-Allen et al. 1995). Resampled to 25 m.	1992 Landsat TM, 1081 rows x 1290 columns from EOSAT corporation. Resampled to 20 m.
Terrain, including slope	Single band, 16-bit Digital Elevation Model (DEM) derived raster from United States Geological Survey (USGS) 7.5 minute quadrangle maps.	Digital Terrain Model from aerial photographs (Aerometric, Inc., Sheboygan, WI, and Construction Engineering Research Laboratory, Champaign, IL, USA, 1985). Supplemented from DEM data (USGS 7.5 minute quadrangle maps).
Geology	Derived raster from vector/polygon data (Hatcher et al. 1992).	7.5 minute, 1:24000 maps (Kentucky Geologic Survey 1985)
Soil	Soil series or soil taxonomy (Hatcher et al. 1992, Moneymaker 1981)	Soil series (Arms et al. 1979, Whitaker and Waters 1986, unpublished Meade County soil survey)
Protected natural areas	Derived raster from vector data (King et al. 1994, Pounds et al. 1993)	Manual map overlay (White et al. 1994)

Table 3. Suitable substrates for limestone glade ecosystems at Fort Knox and the ORR.

SOIL ORDER		SOIL SUBORDER		ORR[1]	FORT KNOX
				SOIL SERIES	
Mollisols	Organic layer and high cation exchange capacity. Usually formed under prairie vegetation.	Lithic Rendolls	Shallow, well drained, rocky soils developed on carbonate bedrock under woodland in temperate climate.	Gladeville	None present
		Lithic Argiudolls	Shallow, well drained, rocky soils developing a clay layer, containing carbonates	not named	Corydon: mapped as Rock outcrop - Corydon complex
Alfisols	Moderate cation exchange, with a defining clay layer. Formed in transitional areas between prairie and forest in moist, temperate climates.	Lithic Hapludalfs	Shallow, well drained, rocky soils developed in moist, temperate climate.	Carbo Upshur variant[2] Capshaw	Caneyville: mapped as Caneyville - Rock outcrop complex and Garmon[3] Caneyville: mapped as Hagerstown[4] Hagerstown
				GEOLOGIC SUBSTRATE	
			Thin layers of limestone resistant to weathering	Chickamauga	Salem Harrodsburg

[1] Soil Types of the ORR are from the Hatcher et al. (1992) geologic survey and data base (this source did not use Soil Series names); Soil Series names are from the Anderson County Soil Survey (Moneymaker 1981).

[2] Soil mapped as Upshur variant also contain areas of Lithic Hapludalfs.

[3] Soil mapped as Garmon (dystric Eutrochrept) contains thin bands of Caneyville-Rock outcrop complex.

[4] Soil mapped as Hagerstown also contains small areas of shallower Caneyville.

Table 4. Importance percentages of highest ranked species on the ORR-Boeing Tract[1].

SPECIES	IMPORTANCE PERCENTAGE[2]
Schizachyrium scoparium	16.4%
Silphium terebinthinaceum	8.8%
Helianthus occidentalis	8.7%
Aster laevis	6.9%
Liatris cylindracea	5.4%
Solidago rigida	4.5%

[1] Data collected at Crowder Cemetery State Natural Area by L. Pounds, J. Baskin, C. Baskin, P. Parr, and M. Cunningham.

[2] Importance percentage = $\frac{\sum(\text{relative density} + \text{relative frequency} + \text{relative dominance or cover})}{3}$

(Mueller-Dombois and Ellenberg 1974)

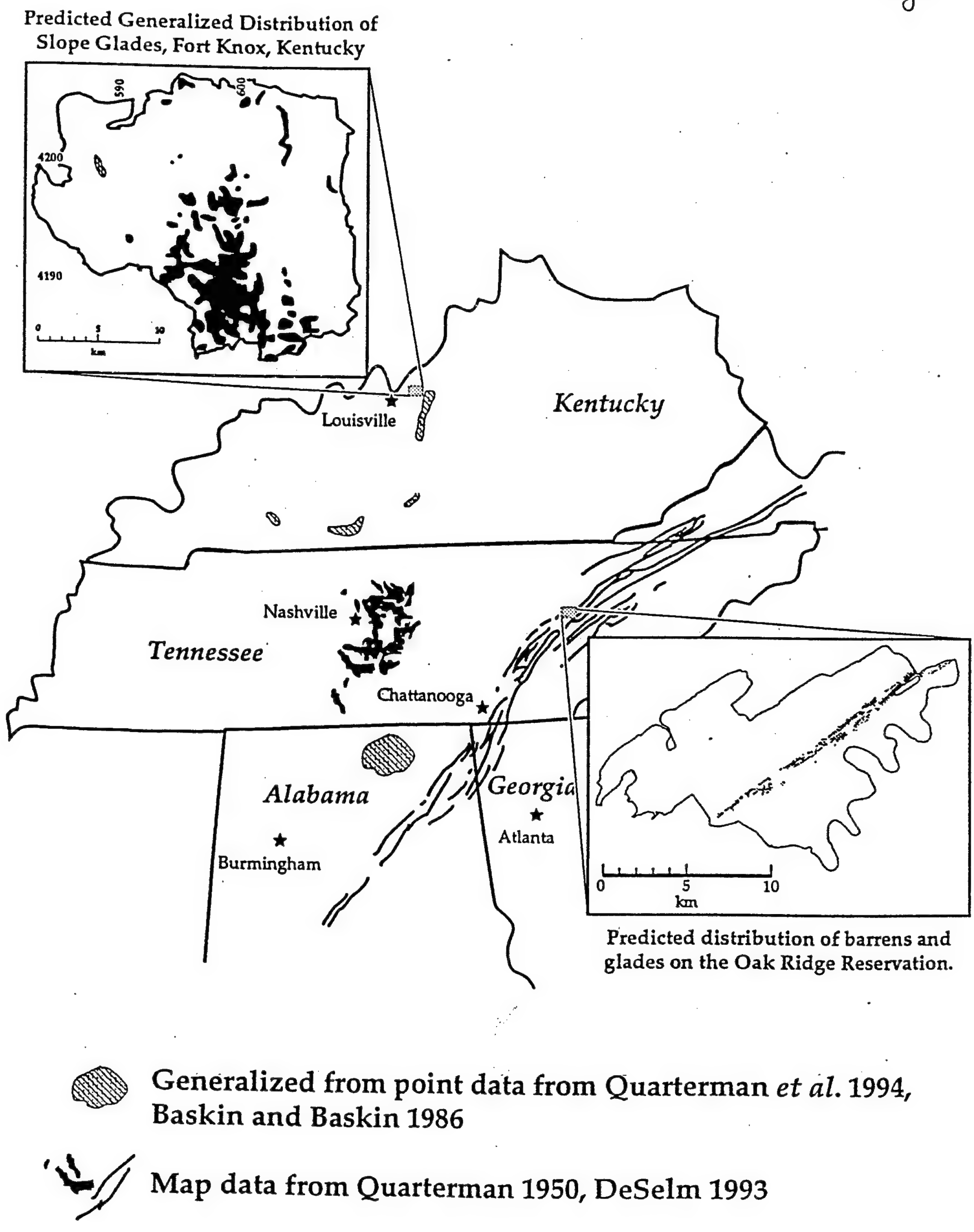
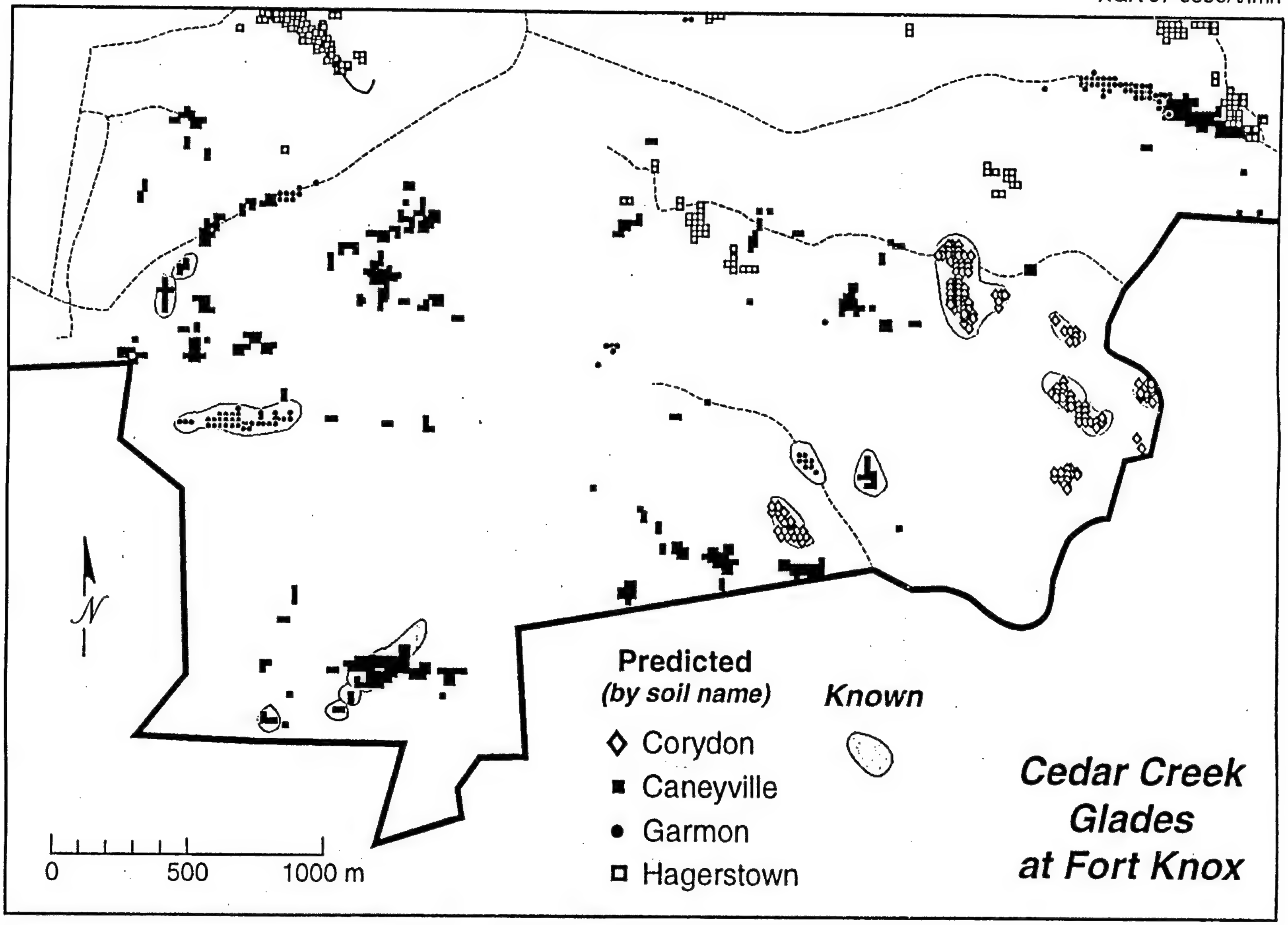

Predicted Generalized Distribution of Slope Glades, Fort Knox, Kentucky
590
600
4200
4190
0
5
10
km
Kentucky
Louisville
Nashville
Tennessee
Chattanooga
Alabama
Georgia
Atlanta
Burmingham
0
5
10
km
Predicted distribution of barrens and glades on the Oak Ridge Reservation.
Generalized from point data from Quarterman *et al.* 1994, Baskin and Baskin 1986
Map data from Quarterman 1950, DeSelm 1993

Fig 2

XGA 97-0850A/lmh



ORNL 97-106287/ lmh

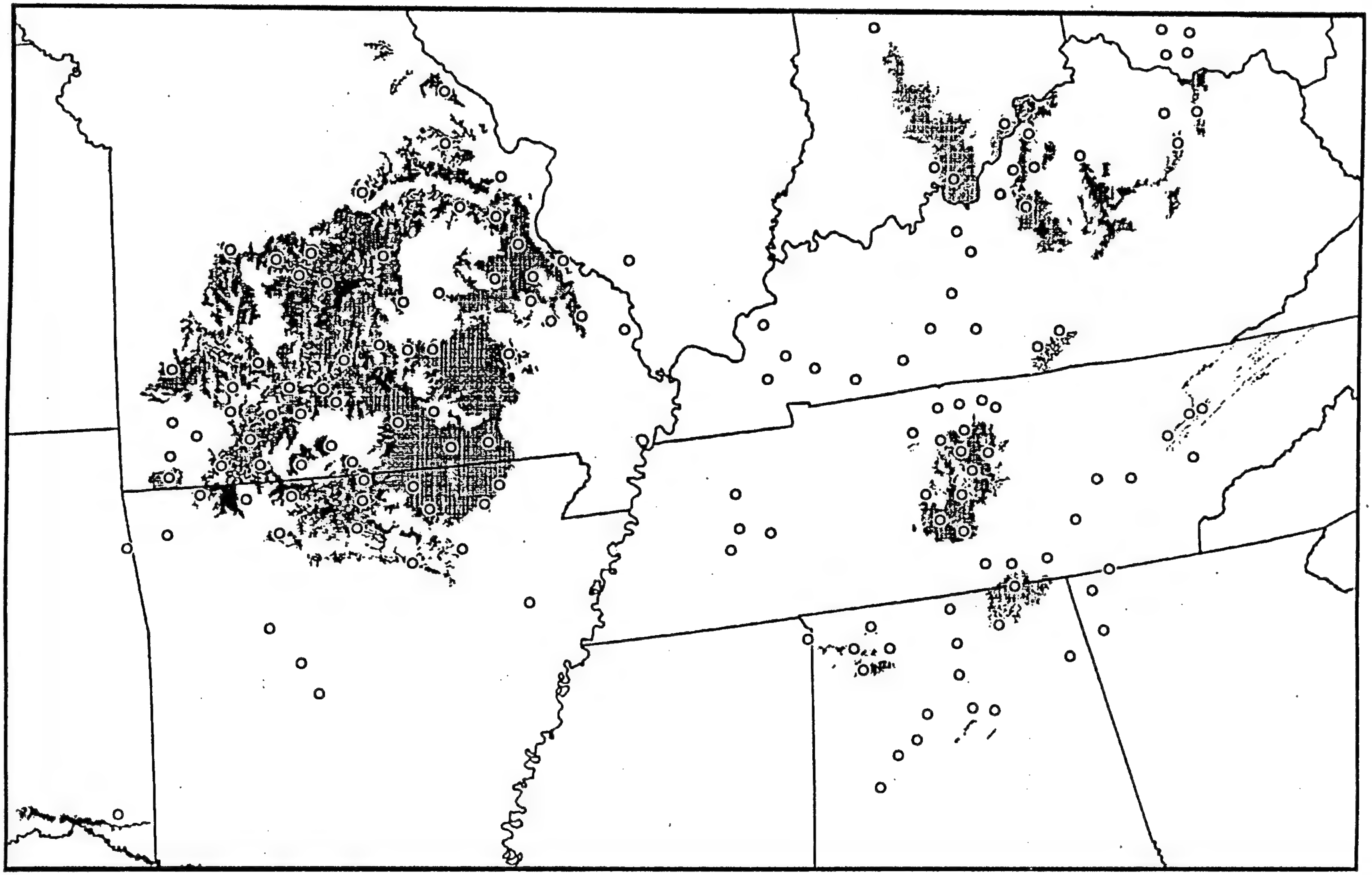
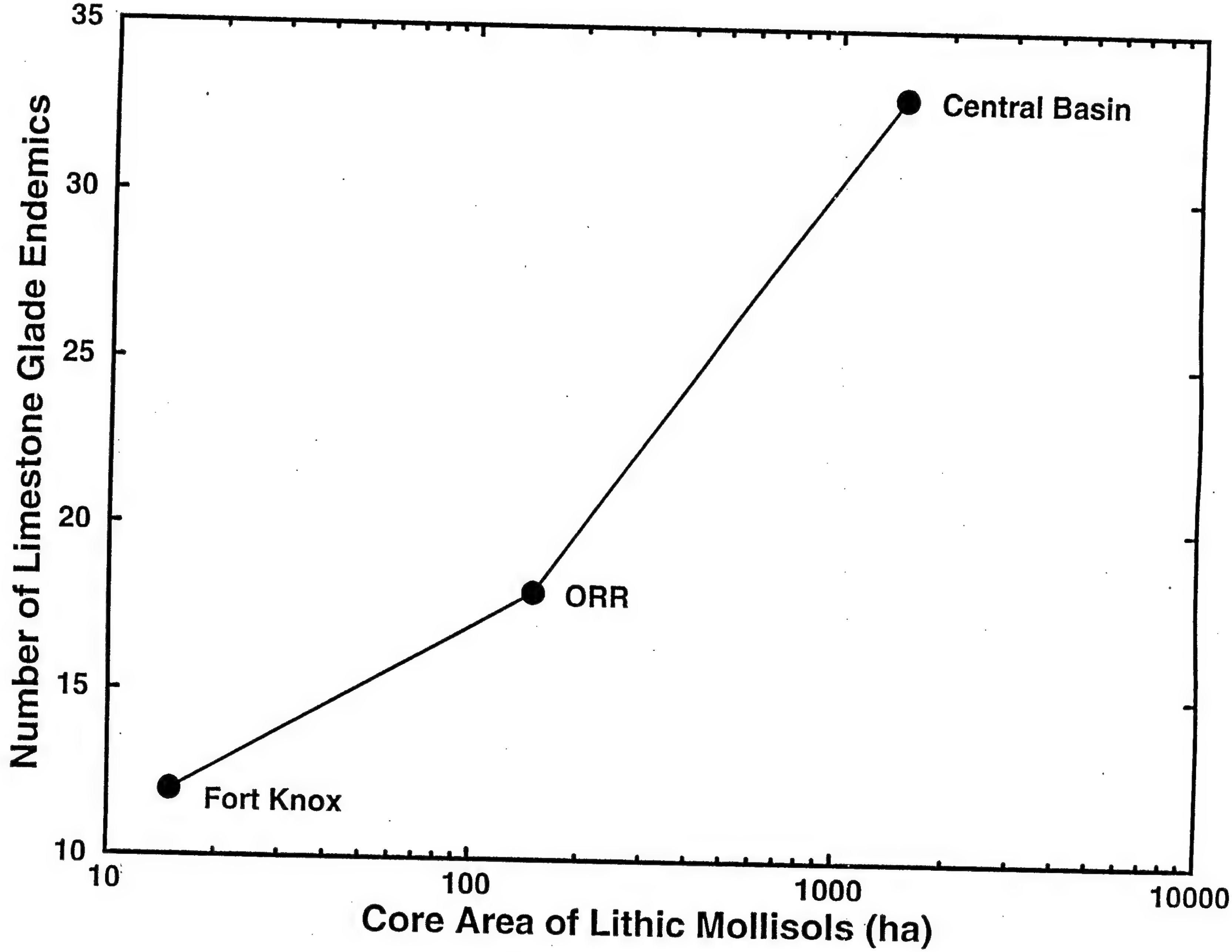


Fig 3


Number of Limestone Glade Endemics
35
30
25
20
15
10
Central Basin
ORR
Fort Knox
10
100
1000
10000
Core Area of Lithic Mollisols (ha)
Fig.

Approach to Terrestrial Modeling

Background

Our objectives are (1) to identify areas within the Neuse River Basin where there is the potential for nitrogen and phosphorus flux from the terrestrial system to the aquatic system (i.e. contributing sources) and (2) to model the seasonality of potential nitrogen and phosphorus flux from terrestrial systems to aquatic systems flowing into the Neuse River. The purpose is to use this information to identify terrestrial sources as contributing factors to harmful algal blooms and Pfiesteria outbreaks. The potential flux of nitrogen and phosphorus from the terrestrial system to the aquatic system is partly a function of the difference between nutrient supply and demand. Nitrogen and phosphorus supplies and demand vary spatially (according to land cover type) and temporally (according to season of the year).

Terrestrial nitrogen cycling is under strong biological controls and simple models that are used to summarize nitrogen cycling in terrestrial ecosystems usually consist of no less than 3 state variables: soil organic matter, available soil nitrogen, and biota (see for example, Cole and Rapp 1981, Nadelhoffer et al. 1985). Similarly, phosphate transformations in soils can be represented by a simple three compartment model which includes adsorbed phosphorus, available phosphorus, and organic matter. The primary inputs to available soil nitrogen and phosphorus are fertilization, atmospheric nitrogen deposition, and mineralization of soil organic matter. The principal losses from available soil nitrogen include leaching losses, denitrification, and ammonia losses through volatilization.

Nitrogen inputs in deposition (atmospheric deposition or fertilization), the release of organically bound nitrogen or phosphorus through mineralization, the adsorption of ammonium-N and orthophosphate to soils, and the uptake of available nitrogen and phosphorus by plants and microorganisms all play some role in determining the amount of excess soil nitrogen and phosphorus that is at risk of loss from terrestrial to aquatic systems. The basic equation for calculating excess soil nitrogen or phosphorus (E, kg/ha) is:

$$E = (F + A + M) - (C + R)$$

where,

F is fertilizer nitrogen or phosphorus (kg/ha),
A is atmospheric nitrogen deposition (kg/ha)
M is net soil nitrogen or phosphorus mineralization (kg/ha),
C is nitrogen or phosphrous adsorbed on exchange surfaces (kg/ha),
R is the ecosystem nitrogen or phosphorus requirement (kg/ha).

This model is consistent with the observation that the

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Running head: Hybrid GIS-Based habitat modeling at Fort Knox · Hargrove et al.

Deductive and Inductive Mapping of Potential Rare Species Habitat on Military Lands using a Geographic Information System[1]

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Abstract: Military lands frequently contain important biological resources such as rare plants and animals and ecologically significant habitat for these species. To provide stewardship of these resources while still maintaining or expanding traditional military activities (e.g., training), land managers must know the location of the resources. We present a series of habitat models utilizing readily-available data in a Geographic Information System (GIS). Our approach combines deductive rules based on spatial data layers such as soil type, underlying geology, and land cover information, with inductive models based on known wildlife sighting locations. We present predictive models for potential Henslow's sparrow (*Ammodramus henslowii*) and cerulean warbler (*Dendroica cerulea*) nesting habitat, cedar barrens communities, and armored vehicle training areas. The models were developed and tested at Fort Knox, KY, USA, but the techniques are transferable to other sites, species, and habitat types. The habitat maps were > 80% accurate, despite inaccuracies in the land cover map (<50% correct). Use of multiple GIS data layers along with inductive extrapolation of sighting locations made the habitat models robust relative to models based only on land cover or remote imagery. Models tended to overpredict habitat slightly; this may be desirable for conservation purposes. The cedar barrens habitat model predicted potential cedar barrens in a larger area than had previously been set aside for cedar barren management. The

Henslow's sparrow model predicted potential nesting habitat for these birds in areas not currently identified by Fort Knox personnel. In both cases, field testing suggested that the broader predictions were valid. GIS-based habitat predictions can focus field work required to verify the presence and status of endangered habitats, and may reduce the costs of future land management activities.

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Key words: *Ammodramus henslowii*, army, barrens, cerulean warbler, *Dendroica cerulea*, Fort Knox, GIS, habitat, Henslow's sparrow, Kentucky, LCTA, map, military, model

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Department of Defense (DoD) lands are managed for military training and conservation of natural resources, but these uses are potentially in conflict. Such potential conflicts must be mitigated without impacting primary training activities. With 10 million hectares under its control (Goodman 1996), the DoD is in a unique position to implement ecosystem management (Mann et al. 1996). A key component of this management is accurate information on the location of habitat for rare and endangered species relative to training activities. GIS-based models offer a method of predicting potential locations of these biological resources, thus focusing field verification efforts and reducing time and expense. GIS-based models can be updated rapidly with newly-acquired information.

Stoms et al. (1992) distinguish between inductive habitat modeling approaches, in which characteristics of locations where species occur are

generalized to the rest of the management area, from deductive rule-building approaches, in which inferences are made from the general to a particular case. Deductive approaches are determined *a priori*, and try to anticipate the organisms by explicitly choosing habitat criteria which are believed to be important. In inductive approaches, habitat choices of a subset of the organisms are observed, and the chosen habitat characteristics are extrapolated to wider areas.

GIS-based habitat models are usually based on an exclusively deductive or inductive approach, but few habitat modeling studies have integrated both techniques. Many habitat models are based on deductive rules involving land cover type and other characteristics. For example, Clark et al. (1993) developed a deductive multivariate model of female black bear (*Ursus americanus*) habitat in the Ozark National Forest based on forest cover and several topographic and spatial parameters. Rudis and Tansey (1995) modeled black bear habitat on a regional basis for the entire southeastern United States using deductive rules based on Forest Inventory Analysis surveys from the U.S. Forest Service.

Inductive methods generalize from sites known to be habitat to the rest of the map. Census data form the foundation for inductive habitat prediction. Homer et al. (1993) used Landsat Thematic Mapper (TM) data to model sage grouse (*Centrocercus urophasianus*) habitat in Northern Utah. Coker and Capen (1995) used aerial surveys of the Green Mountain National Forest along with field census data to develop an inductive model of cowbird (*Molothrus ater*) use of disturbance patches in the forest. Knick and Dyer (1997) analyzed remotely-sensed shrub vegetation within 1 km of black-tailed jackrabbit (*Lepus*

californicus) sightings to inductively predict habitat and estimate loss to large-scale fires.

Lauver and Whistler (1993) used a hierarchical inductive classification of Landsat TM data to identify native grasslands in eastern Kansas, USA. Discriminant analysis of ground occurrence data was extrapolated to distinguish high-quality from low-quality grasslands. Seventy-seven previously unknown natural grassland areas were identified, nine of which contained populations of the Federally-threatened Mead's milkweed (*Asclepias meadii*).

In one of the few habitat modeling studies to have integrated both deductive and inductive approaches, Sperduto and Congalton (1996) used GIS to predict potential habitat for the small whorled pogonia (*Isotria medeoloides*), the rarest orchid in eastern North America north of Florida. Using a weighted hybrid model which included slope, aspect, and soil characteristics with Landsat TM Band 4 reflectance signatures generated from known orchid locations, they correctly predicted 78% of the known occurrence sites for this orchid in New Hampshire and Maine.

Lowell et al. (1989) also used a hybrid GIS approach to predict cedar barren communities within the Hercules Glades Wilderness Area, Missouri at five intervals over a 48-year period. They identified physiographic factors correlated with the presence of glades using a modified Chi-squared analysis, which indicated a strong positive association with shallow Gasconade soil, elevations from 305-365 m, and southern and southwesterly aspects. This model of physiographic and edaphic factors allowed them to predict 93% of the glades known to be present in their study area (Lowell et al. 1989).

In this paper, we use a combination of inductive and deductive GIS modeling approaches to predict potential habitat for two bird species, Henslow's sparrow (*Ammodramus henslowii*) and cerulean warbler (*Dendroica cerulea*), and for limestone cedar barren communities at the Fort Knox Military Reservation, Fort Knox, KY. Both birds were previously listed as Federal category 2 candidate species, and Henslow's sparrow is listed as a special concern in Kentucky. The slope glade habitat at Fort Knox contains several state-listed and previous Federal candidate species of plants. In this hybrid approach we make use of a number of spatial data layers, including soils and geology, to produce robust models that do not rely so heavily on the accuracy of any given layer (Stoms et al. 1992).

Limestone cedar barrens are of conservation interest because of their rarity and importance as potential habitat for several rare plant species, invertebrates, and other biota (Noss 1992). Cedar barrens, sometimes referred to as slope glades, limestone hillside glades, or xeric limestone prairies, occur in sparse woodlands usually including red cedar (*Juniperus virginiana*). Barrens are characterized by shallow, flaggy limestone soils, with limestone occurring at or near the surface of the ground. Biota of limestone barrens have not been examined in detail, except for plants (DeSelm et al. 1969, Baskin and Baskin 1978, 1986, DeSelm 1989, 1994, Baskin et al. 1994, Cunningham et al. 1993, DeSelm and Murdock 1993). Cedar barrens support a relatively distinct flora, and most cedar barren communities have a high degree of taxonomic similarity (DeSelm et al. 1969). While most cedar barrens are small (< 1 ha), they represent critical habitat for several rare plant species, including Eggleston's violet (*Viola egglestonii*, Kentucky special concern), slender blazing

star (*Liatris cylindracea*, Kentucky threatened), and the Great Plains Ladies-tresses (*Spiranthes magnicamporum*, Kentucky threatened).

In the eastern United States, Henslow's sparrow breeds in northern and central Kentucky and Virginia in grassland habitat (Hamel 1992). Henslow's sparrow nesting sites are associated with relatively productive dense, tall grasslands or hay fields with adequate moisture which are not mowed or burned annually and have little or no woody vegetation (Robins 1971, Zimmerman 1988, Hamel 1992). Historically, populations of Henslow's sparrow west of the Appalachians were primarily associated with native tall grass prairies and forest prairie mosaics (Graber 1968, Zimmerman 1988). This sparrow's gradual but persistent decline has been attributed to the decreasing availability of standing dead vegetation in open grassland (Zimmerman 1988).

Nesting habitat for cerulean warblers (*Dendroica cerulea*) consists of extensive tracts of tall, mature, hardwood trees (Bent 1953, Robbins et al. 1989a, Hamel 1992). This warbler is found in a wide range of forested habitats, including bottomland hardwoods of the coastal plain and Ohio River drainage, and steep to hilly slopes of the Cumberland Mountains (Robbins et al. 1989a, Hamel 1992). Nesting habitat includes many forest types in both uplands and bottom lands, usually without much underbrush (Bent 1953, Robbins et al. 1989b, Hamel 1992). Forest stands selected for nesting are reported to contain many live stems > 30 cm dbh (50-150 cm), with old growth canopy 20-30m high, and canopy closure >85% (Robbins et al. 1989b).

Since the main activity of biological impact at Fort Knox is training with armored vehicles, we use the same habitat techniques to predict areas where

such disturbances can potentially occur. We consider the non-biological "habitat" requirements for tracked armored vehicles in the same way that we model the land characteristics required for biological species. Thus, the same GIS-based deductive methods used for biological predictions are extended for predicting land use suitability for tank movement and training.

We tested the accuracy of the land cover and habitat maps by comparing field observations at known locations with predictions from the models at those locations. Accuracy assessment in the field was map-directed; points were dropped randomly on each category in the map, and field teams were sent to test the map at those locations.

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STUDY AREA

The Fort Knox reservation is a 44,595 ha U.S. Army installation in north central Kentucky, USA, and contains parts of Bullitt, Hardin, and Meade counties. The reservation adjoins the Ohio River, and is drained by the Salt River and its tributary, the Rolling Fork. Many smaller streams are present in the hilly terrain.

The basic geologic structure at Fort Knox is Devonian shale, overlain by layers of limestone interspersed with layers of dolomite and silty shale. Most of the Fort Knox is underlain by St. Louis Limestone and Salem Limestone, with karst features throughout (KGS 1985). Most soils are Alfisols with some Inceptisols in complex patterns on steep hillsides (Arns et al. 1979, Whitaker and Waters 1986). A few small areas of Mollisols are also present.

Most of Fort Knox is second-growth deciduous forest. There are 18 training areas just inside the perimeter of Fort Knox where the Army conducts both vehicle-based and on-foot training. Half of the reservation, about 21,332 ha, is an impact area for ordnance where only Army personnel are permitted. Almost all of the floodplains surrounding the Salt River and Rolling Fork lie within this central impact area. Non-forested areas include the cantonment area of the base, and the towns of Radcliff, Muldraugh, and West Point, KY, are also within or adjacent to the reservation. The western third of the reservation has good road accessibility, but there is only limited gravel road access to the northern and southern training areas.

METHODS

Deductive GIS methods combine spatially co-registered stacks of maps of edaphic, physiographic, and reflectance properties. Selected conditions from each overlay map were combined, usually by exclusion or intersection, using the Geographic Resources Analysis Support System (GRASS 4.1 1993). The habitat specifications used in our research were recipes of edaphic and geologic factors, terrain characteristics, and land use/land cover types. Our aim was to capture the essential factors defining potential habitat.

Potential habitat was primarily defined by suitable vegetation composition and structure, and potential vegetation depends on soil properties. Our deductive approach to predicting habitats at Fort Knox was to identify edaphic characteristics from county-level soil surveys which would allow appropriate vegetation, and included presence of diagnostic horizons (taxonomic class), soil depth, woodland suitability class (incorporating slope, fertility, soil depth, water availability, and extent of erosion), and depth to water table or tendency to flood. Appropriate soil series were used to predict whether vegetation appropriate for habitat could be supported by the type of soil present at a particular map location. These predictions were then intersected with the land cover map to determine whether suitable land cover was present. Land-use history was not available at the time of this study, so the age of vegetation in predicted habitats was unknown.

Available Data Sources

GIS maps of many features were already available for Fort Knox, as with many military and Federal installations. We developed a land cover map

from a Landsat Thematic Mapper (TM) image (EOSAT Corporation), taken on Sept. 12, 1992, from path 021, row 033, consisting of 1081 rows x 1290 columns, with a sun elevation of 47 degrees, sun azimuth 135 degrees, which covered the entire Fort Knox reservation and was essentially cloud-free. The Fort Knox image consists of 6 bands with an original resolution of 30 m (Band 6 was not included because of coarser resolution), and had been georegistered and resampled to 20 m resolution prior to this project.

Ground-based field census or sighting data are required to use inductive approaches to habitat projection. Most U.S. military bases are participating in the Land Condition Trend Analysis (LCTA) data collection program, in which randomly located, 100 m long transects on pre-selected vegetation/soil series combinations are repeatedly sampled for vegetation, birds, soil characteristics, and disturbance (Environmental Management Division 1994). LCTA data were collected at Fort Knox repeatedly from 1991-1994.

We used digitized versions of soil surveys from Hardin and Bullit counties (Arns et al. 1979, and Whitaker and Waters 1986, respectively), but added Meade county information from a draft version of the unpublished county soil survey. We combined the two map layers to produce a complete soil coverage for Fort Knox. A digitized version of 7.5 minute 1:24000 maps from the Kentucky Geologic Survey (KGS 1985) was used as a geology layer.

A digital terrain model was developed by Aerometric, Inc., Sheboygan, WI, USA from aerial photos taken in 1985 (64 stereo pairs, 1:24000 scale, 12,000 ft altitude) and rectified by the Construction Engineering Research Laboratory, Champaign, IL, USA. The horizontal resolution is 10 m, with a vertical resolution of 0.1 m. A small portion of the reservation was not done

photogrammetrically, but was patched in from 30 m Digital Elevation Model (DEM) data available from USGS. We spline-smoothed the terrain model within this lower-resolution section to 10 m resolution using the GRASS program s.surf.2d (Mitasova and Hofierka 1993). We derived percent slope and aspect models from the terrain model using standard GIS tools (GRASS 4.1 1993).

Land Cover

All of the GIS-based habitat models relied to some degree on land cover. The 1992 Landsat TM image and the LCTA data for Fort Knox were used to develop spectral signatures for a supervised land cover classification of the TM image (Figure 1). We used a preliminary summary of the LCTA data set (Environmental Management Division, Fort Knox, 1994) to classify vegetation in each LCTA plot into the USGS land cover scheme of Anderson et al. (1976). The summary lists the predominant vegetation type within each LCTA plot. One non-Anderson category was retained from the LCTA plot summaries: maintained grass, described as present in periodically mowed firing ranges, lawns and roadsides. Thus, the 152 LCTA plots with GPS locations (converted to North American Datum 27 for map registration) were unambiguously grouped into nine categories: deciduous forest, mixed forest, evergreen forest, transitional, barren, urban, water, and maintained grass.

We used lakes and major rivers, as well as primary roads, from pre-existing GIS layers to provide spectral signature sites for water and urban categories. The outermost cells of these urban and water polygon features were discarded to improve the spectral signatures for these classes. An

iterative maximum-likelihood discriminant function algorithm was used to classify each cell in the image (i.maxlik program, GRASS 4.1 1993).

Initially, the classified map included areas of known cropland and ornamental lawn grass as maintained grassland. A second set of spectral signature areas were delineated for these two land cover types, and the classification was repeated. The resultant 10-category map contained no conspicuous classification problems, and can be seen at http://www.esd.ornl.gov/programs/SERDP/knox92.gif.

Cedar Barrens

Dale et al. (1997) used a GIS to deductively predict potential cedar barrens within the Oak Ridge DOE Reservation by intersecting soil, slope, geology, and land use characteristics. They defined potential cedar barren habitat as the intersection of specified Mollisols (lithic Rendolls) or lithic and typic Hapludalf soil series, along with thin- and medium-bedded Chickamauga limestone residuum and colluvium geology, slopes less than 25%, and land use/land cover types of urban, pasture, barren land, mixed forest, or transitional areas. The spectral signature for exposed limestone within barrens resembles that of urban gravel or concrete (Dale et al. 1997). Dale et al. (1997) found that Mollisols were always associated with limestone cedar barrens, indicating that these sites have long been dominated by herbaceous vegetation. However, some cedar barren communities were located not on Mollisols, but on Alfisols, indicating a mixed history of vegetation cover.

We hypothesized that limestone barrens at Fort Knox would most likely occur on Mollisols or Alfisols, but would not be found on Ultisols. From these

edaphic principles, we hypothesized that the Corydon (RoE) and Fairmount (FkF, FnF) lithic Mollisols, the Cynthiana (FlE) lithic Hapludalf, the Caneyville (CbD, CnD, and CnE), Fredonia (FdC), and Hagerstown (HnB, HnC, and HnD) typic Hapludalfs would be associated with cedar barrens. Thus, potential cedar barren communities at Fort Knox were deductively defined as one of the above soil types and either transitional, barren, urban, maintained grass, cropland, or lawn grass land use categories, with slope less than or equal to 30%. Geologic categories required for potential barrens were predominantly thin- to medium-bedded limestone types, including Harrodsburg, Salem, Ste. Genevieve, or St. Louis formations, or argillaceous or crinoidal limestone (Figure 2).

Fort Knox has established a preserve for cedar barrens in the southernmost tip of the reservation, and the management plan includes a coarse map of cedar barrens within the Cedar Creek Glades Preserve (White 1993, Figure 3, bottom). We made iterative edaphic and physiographic refinements in the cedar barrens habitat specification (Figure 2) based on comparison of predicted prospective barrens with mapped barrens locations within the barren preserve (Figure 3).

The addition of Garmon soils underlain by Harrodsburg or Salem limestone resulted in a site-specific accuracy (Mead and Szajgin 1982) of predicted barrens locations of nearly 100% for all known cedar barrens inside the Cedar Creek Glades Preserve (Figure 3). The Garmon soil series, a dystric Eutrochrept Inseptisol, is reported by Baskin et al. (1994) as the primary series on which xeric limestone prairies occur in Hardin and LaRue counties, KY. The soils mapped as Garmon in the Hardin and LaRue county soil

surveys contain thin bands of Caneyville-Rock outcrop complex (Arns et al. 1979). These Caneyville-Rock outcrop inclusions only occur where Salem and Harrodsburg limestone were present. Thus, the Garmon (GmE, GmF) dystric Eutrochrept was included in the cedar barren specification, but only where underlain by Harrodsburg or Salem limestone.

Henslow's Sparrow (*Ammodramus henslowii*)

Two substantially independent lines of reasoning, one deductive and one inductive, were used to develop predictions for prospective Henslow's sparrow habitat (Figure 4). The intersection of these predictions from different logical approaches was used as the final prediction.

Deductive prediction of Henslow's sparrow habitat at Fort Knox was based on identifying sites which could support dense grass vegetation. Soils identified as potentially suitable to support dense stands of grass included the Mollisols and mollic Alfisols, and a number of Alfisols (Hagerstown, Markland, Beasely, Lowell, Alford, Elk, Wellston, Crider, Sonora, Vertrees, Baxter, Cumberland, Gatton, Nicholson, Otwell, Zanesville, Lawrence, and Sadler). Soils that were too wet (water table too close to the surface or frequently flooded), too dry (shallow), or too eroded were excluded. Severely eroded phases of Baxter and Beasely were also excluded. Pixels with unsuitable land cover were then eliminated as potential Henslow's sparrow habitat. Transitional, barren, maintained grass or lawn grass land cover types were considered potentially suitable.

At Fort Knox, where Henslow's sparrow is a Kentucky state-listed species of special concern, grasslands near the Goudmon Army Airfield are

managed as a protected area for a breeding population of these birds. A 100 m radius circle containing this nesting population (centered at 590200E, 4196500N UTM meters, Zone 16) was used to inductively identify areas with similar spectral characteristics elsewhere within the reservation. Because a single habitat class is not sufficient for discriminating a binary habitat map, the maximum likelihood classification algorithm was run with the single signature on the raw Landsat TM spectral data, and a Chi-squared test was performed on each discriminant result at every cell. The reject threshold map that resulted contained the confidence level at which each cell in the map was classified. Cells that had less than a 5% probability of being correctly assigned to the Henslow's sparrow habitat class were defined as *not* Henslow's sparrow habitat. A spectral signature was developed for these non-habitat cells, and the maximum likelihood classification was repeated to produce a binary habitat prediction. Because the nesting habitat is believed to be limiting for this species (Zimmerman 1988), we used the intersection of the deductive and inductive layers as the predicted habitat map.

Cerulean Warbler (*Dendroica cerulea*)

We used a similar hybrid of inductive and deductive approaches for predicting potential cerulean warbler nesting habitat. Our approach combined known nesting locations, remote imagery, information from the literature, land cover data, and soil survey interpretations.

We deduced that the tall trees required by cerulean warblers would only be produced on soils with adequate depth and moisture. Soil site index, which is the height that a mature tree of a given species will reach by age 50,

provides an integrated index of rooting depth, soil moisture, and fertility. Soils in moderate to low productivity classes generally have site indexes insufficient to produce the tall trees required by cerulean warblers. Sites in woodland suitability classes 1, 2, and 3 generally have a hardwood site index of more than 18 m (59 ft) in uplands and more than 24 m (79 ft) in bottom lands. Most of the forested soils on uplands and in valleys at Fort Knox were in these high suitability classes, and could produce trees tall enough to be cerulean warbler habitat. Stand age data were not available for the prediction.

Soils deemed unlikely to support taller trees included severely-eroded Beasley silt clay loam on 6-20% slopes (BfC3, BfD3), severely eroded Eden flaggy silty clay on 20-30% slopes (EdE3), Garmon silt loam on 25-60% slopes (GmE), and soils mapped as complex mixtures of Caneyville, Faywood, Cynthiana, Fairmount, and Woolper series (Cb, Cn, Fl, Fn). Soils identified as potentially suitable were then compared with deciduous forest land cover. Pixels with either unsuitable land cover or unsuitable soil types were eliminated. Only deciduous forest was considered potentially suitable land cover. This intersection produced a prospective cerulean warbler habitat model from the deductive line of reasoning.

In the Endangered Species Survey of Fort Knox, White et al. (1994) identified spatial coordinates for three locations and two transect endpoints where cerulean warblers were seen or heard in the field during the breeding season (603250E, 4203000N; 607900E, 4202700N; 600625E, 4201875N; 586200E, 4200500N; 585500E, 4203225N meters, UTM Zone 16). A spectral signature was developed for these known locations and the eight cells surrounding them. As with Henslow's sparrow, cells with less than 5%

probability of being correctly assigned to cerulean warbler habitat were defined as *non*-habitat, and the maximum likelihood algorithm was used to classify the Landsat TM image using the signature for these two classes. As with the Henslow's sparrow, the deductive edaphic/land cover approach was intersected with the inductive extrapolation of known field sites, and only areas common to both approaches were included in the final potential Cerulean warbler habitat map.

Tank Movement/Training

Deductive, rule-based techniques are sufficiently flexible that they can be used to predict locations where tank training, the main disturbance impacting habitats at Fort Knox, might occur (Figure 2). Becoming mired in mud is one potential movement-limiting factor for tanks at Fort Knox (Dames & Moore 1979). In addition, the metal cleats on treads have little traction or steerage on rocky outcrops not covered by soil (Dames & Moore 1979). Actual slope limits for particular types of tracked vehicles depend on gross vehicle weight and attitude orientation relative to the incline. While tracked vehicles might be able to negotiate more rugged terrain,our recipe represents areas ideal for tank training, where risk of becoming mired would be low.

Armored vehicles can drive over shrubby vegetation and saplings, but cannot move through heavily forested land cover types. Furthermore, Fort Knox prohibits armored vehicles from approaching rivers, creeks, and lakes (except at prepared crossings) to protect ecologically important riparian habitats and water quality, as well as to avoid flooding and bogging hazards. Thus, we defined potential ideal tank movement/training areas (1) to be within

the Ft. Knox reservation boundary; (2) to be not less than 20 m from rivers, creeks, and lakes; (3) to have slope less than or equal to 15%; (4) to be transitional, barren, urban, cropland, or lawn grass land cover categories, and (5) not to have soil types with rock outcrops, gullied land, pits, or that are loose or frequently flooded (i.e., muddy)(Figure 2).

Field testing and accuracy assessment

Because the impact area is only open to Army personnel, it was excluded from the field testing. Field testing was restricted to points within a 50 m buffer on either side of roads to maximize the number of points visited. Points of each habitat and land cover type were selected randomly within the road buffers. Map-directed assessment of accuracy is a more stringent test than field-directed assessments, in which field crews select points for testing. Choices made in the field are likely to favor the centers of large, homogeneous, representative examples of a particular cover type, whereas random selection from the map may choose test points along edges or isolated small islands of cells.

At each point, field teams obtained a location from a portable Global Positioning System (GPS) unit, determined the land cover type of the 20m pixel in which they were located, and noted whether or not each habitat type was present. Field accuracy assessment was done blind; the field teams did not know which land cover category or habitat type had been predicted for the point. Photos were taken at each field site. Each team collected at least 20 position fixes, once every 10 seconds, at each point location. GPS locations were differentially corrected against a base station at the University of

Kentucky, Louisville. Predicted tank movement/training areas were not included in the field tests, since they were predicted only to gauge their potential impact on the other habitats.

To ensure that all field teams had a common perception of the habitat and land cover types, all teams were trained using examples during the first field day. In addition, a set of key criteria were used as a litmus test for recognizing each habitat type during the accuracy assessment (Table 1).

RESULTS AND DISCUSSION

Henslow's sparrow nesting habitat (Figure 5) was the rarest of the habitats predicted (838 ha), followed by cedar barrens habitat (1100 ha; Fig. 5), and tank movement/training areas (7312 ha; Fig. 6). Potential cerulean warbler habitat (Figure 6) was much more extensive (13430 ha), accounting for ~30% of the reservation.

The cerulean and tank training maps (Figure 6) certainly overpredict the amount of habitat actually useable. Robbins et al. (1989a) report that the "area at which probability of occurrence is maximum" for cerulean warblers is more than 3000 ha, and that the probability of finding the birds is reduced by half in patches less than 700 ha. No minimum usable area habitat requirements were specified in our potential habitat predictions. Inclusion of such requirements would severely restrict the potential warbler habitat. Similarly, some areas designated as ideal for tank training, such as the cantonment area (Figure 6, in the west-central reservation), are suitable but clearly impracticable or unavailable for other reasons.

Field accessibility necessarily biased the testing sample, particularly because of the impact area. For example, lawn grass and maintained grass made up 22% of the sites tested, but make up <10% of the total area at Fort Knox based on the land cover map. Similarly, 25% of the sites tested were transitional, yet this category comprises only 4% of Fort Knox, according to the land cover map. Most of the current cerulean warbler habitat at Fort Knox is within the untestable impact area along the Salt River in riparian forest (White et al. 1994).

A two by two error matrix, with map predictions as rows and field results as columns (Tables 2, 3, and 4), was used to determine the number of times the land cover map and models agreed with field observations (Congalton 1991). A perfect map would have all nonzero counts along the diagonal of the error matrix. Overall accuracy is the sum of counts along the diagonal divided by the total number of tested sites in the matrix. Congalton (1991) also defines user's accuracy, in which each diagonal count is divided by the column total, and producer's accuracy, which is each diagonal value divided by the row total.

The off-diagonal errors are of two types; either we predict that a cell is not habitat when it is, or we predict a cell is habitat when it is not. The former type is an error of omission (Congalton 1991), whereas the latter is an error of commission. When predicting potential habitat for rare species, the consequences of omission are severe relative to those of commission. Wildlife managers would usually prefer to mistakenly include as potential habitat areas that are unsuitable than to miss suitable area.

The land cover map accuracy was poor (34% overall). The overall accuracy improved to 49% when the three forest types (deciduous, mixed, and evergreen) were combined into a single broad forest category (producer's accuracy 87%, user's accuracy 77%). Differentiation among mixed-age second-growth forest types was difficult from a single "leaves-on" Landsat TM image. All categories except lumped forest and lawn grass (80%) had low producer's accuracies.

Errors from the relatively small spectral signature set (152 points), errors in lumping the LCTA summaries into land cover categories, and errors in image registration likely contributed to the relatively poor accuracy of the land cover map. The LCTA plot vegetation was classified solely on the basis of the summary descriptions. Also, using roads for urban spectral signatures may have led to the misclassification of other categories as urban.

Overall accuracy was high for all three habitat models (92%, 83%, and 87%, Tables 2, 3, and 4), despite the low accuracy of the land cover map. All three models were highly accurate at predicting non-habitat (93%, 85% and 87% user's accuracy, Tables 2, 3, and 4). This is an important capability for models used to plan potentially disturbing activities like military training. Because all three habitats are rare, many more non-habitat sites were tested than habitat sites for each map. The models were less accurate at predicting these rare habitat locations (40%, 40%, and 100% user's accuracy), but the small number of tested habitat sites (11 of 142) makes the interpretation of habitat prediction accuracy difficult. Additional field testing of rare habitat locations would be required (particularly for cedar barrens) to make definitive statements about the habitat prediction accuracy of the models.

The Henslow's sparrow model predicted potential habitat at 11 test sites, only two of which were suitable (Table 2). Thus, overprediction occurred in 9 of 142 cases (6%). The model failed to predict Henslow's habitat when it was present only at 3 test sites. Thus, the model correctly predicted 98% of the non-habitat; errors of omission were low.

Inaccuracies in the land cover map did not substantially degrade the accuracy of the Henslow's sparrow model in predicting habitat. Of the nine pixels where sparrow habitat was predicted but did not occur, only two were of a land cover type (deciduous forest) not included in the habitat model. All three pixels where habitat existed but was not predicted had land cover types that could support sparrow habitat.

The cerulean warbler model (Table 3) overpredicted in 21 of 142 test sites (15% commission errors); omissions were limited to 3 sites (2%). Six of the 21 overpredicted sites and two of the three omitted sites were missed because of inaccuracies in the land cover map.

Improving the land cover map would have reduced underprediction of cerulean warbler habitat even further. Producer's accuracy for cerulean warbler habitat could have been significantly improved by incorporating some measure of stand age into the model. The forests at Fort Knox are primarily second growth, with trees that are too small for cerulean warblers. The site index used by the model predicts that trees of sufficient size can be produced on the site, but a map of stand age is needed to determine whether the forests had actually developed the tree size and canopy characteristics required by the birds.

The cedar barrens model (Table 4) predicted that 19 of the field test sites were potential cedar barrens. Only one site was actually classified as habitat by the field teams; this cedar barren community was heretofore unknown (594374N, 4190726E UTM meters, Zone 16). *Post hoc* review of photographs from the predicted test sites suggested that 11 of the 19 had the correct substrate, but typical barrens vegetation was not present because of disturbance. Including these 11 potential-but-disturbed cedar barrens sites, the cedar barrens model would have been 95% correct overall. Without the 11 disturbed sites, errors of commission (overprediction) were limited to 7 of 142 sites (5%); no actual cedar barrens were omitted. Four of the seven overpredictions were incorrect because the land cover map had misclassified them as forest.

The hybrid inductive and deductive habitat models performed better than typical single-approach or single-layer models. Both hybrid models were much more accurate than many non-hybrid models reported in the literature, and all three models had fewer omissions than commission errors. Lauver and Whistler (1993) reported commission errors of 43% in their Landsat-based inductive predictions of high-quality grasslands in eastern Kansas. They reported that commission errors range from 26 to 36% in previous work using GIS to identify natural areas. Using pixels withheld from training, overall accuracy in their study was 75%, lower than for all three models reported here.

The hybrid models were accurate despite the poor land cover map. The relative insensitivity of the habitat predictions to land cover inaccuracies may result from the inclusion of the inductive approaches, or may be because the

deductive approaches utilized multiple layers, one or more of which were sufficient to positively influence the accuracy of the habitat maps.

MANAGEMENT IMPLICATIONS

Several conclusions specific to management of habitat at Fort Knox are significant. Our field test confirmed that cedar barrens exist in at least one area not previously identified. The field test of our Henslow's sparrow model confirms that predicted potential nesting habitat exists in areas other than the known airfield location. The cerulean warbler model overpredicted habitat because 1) minimum area requirements for foraging, and 2) the age of tree stands were not included in the model. Fragmented potential habitat may be unusable (Forman and Godron 1986). Based on the extensive potential habitat prediction, cerulean warbler populations could increase at Fort Knox if young second-growth forests are preserved and allowed to mature.

The prediction techniques were sufficiently general that they could be used not only to predict habitat, but also to predict the main military activity, tank training, impacting habitat at Fort Knox. Potential tank training areas shared a 27% overlap with Henslow's sparrow nesting habitat, the rarest habitat predicted in this study. Cedar barrens and cerulean warbler habitat, as defined here, were exclusive of ideal areas for tank maneuvers. Cedar barrens may actually require some disturbance like fire to persist and prevent woody succession (Lowell and Astroth 1989, DeSelm and Murdock 1993). An animated fly-around of Fort Knox showing potential tank movement areas relative to potential cedar barrens habitat can be seen at http://www.esd.ornl.gov/programs/SERDP/knox.mpg.

Several advantages resulted from the use of the hybrid habitat prediction techniques. A combined approach using deductive and inductive logic resulted in higher accuracy than either technique alone. Habitat predictions based on multiple data layers and on inductively-developed criteria were robust and relatively insensitive to errors in the land cover map. Additional ground-based sites for spectral signature development (i.e., full LCTA plot data), or additional remotely-sensed imagery could improve inductive approaches to land cover map and habitat models. The next challenge to GIS-based habitat modeling will be to estimate habitat quality to support modeling of population demographics (e.g., Liu 1995, King et al. 1997).

Hybrid GIS techniques for habitat prediction work for inaccessible areas where direct census is not possible. Many military bases and certain other Federal lands have substantial areas that are closed to the public and may be available for wildlife (Mann and Kitchings 1982, White et al. 1994). For example, the impact zone at Fort Knox contained 67% of the predicted cedar barren habitat, 43% of the predicted Henslow's sparrow nesting habitat, and 46% of the predicted cerulean warbler habitat. Habitat censusing in impact areas is limited to indirect remotely-sensed inferential or inductive techniques like those described here. The hazards which preclude access to this area guarantee that, except for military uses, the area will remain unaffected by other human purposes.

The habitat prediction techniques should be adjusted for the ultimate uses of their predictions. For the purposes of habitat conservation, slight overprediction of habitat may be desirable. On the other hand, the unnecessary restriction of impact activities like military training is to be

minimized. For the estimation of rare species demographics, any overestimation of habitat may make rare populations appear larger than they are.

These are important implications, both in terms of specific results for these rare habitats on DoD lands and in terms of broader applicability of the hybrid habitat modeling technique to other species and locations. Similar models can be constructed for other species if sufficient information concerning habitat requirements is available. With adjustments to reflect local soils and known habitat, these techniques are portable to any site where these species or communities are important.

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Table 1. Key characteristics used as litmus tests for identification Henslow's sparrow (*Ammodramus henslowii*) and cerulean warbler (*Dendroica cerulea*) nesting habitat, and cedar barren communities during field testing of GIS-based potential habitat maps at Fort Knox, KY, USA, 1996.

Cedar Barrens	1. Substrate is either thin shaley soil containing many flaggy (flat) bits of thin rock or is relatively flat massive pieces of rock. If rock fragments are chert, or if site is a stream bed or a cliff, or if standing water is present, it is not a cedar barren.
	2. Vegetation includes key species such as little bluestem (*Schizachyrium scoparium*), few-headed blazing star (*Liatris cylindracea*), prairie coneflower (*Echinacea pallida*), whorled milkweed (*Asclepias verticillata*), or spiked lobelia (*Lobelia spicata*). Woody species may or may not be present.
Henslow's sparrow	1. Dense grass, at least 60 cm (2 ft) tall, with no soil visible. Grasses may be in bunches with litter-covered soil between clumps, but canopy of grass is closed.
	2. Presence of at least the previous year's unmown dead grass.
	3. No standing water.
	4. No more than 1 sapling tree per 100 m^2

Cerulean warbler	1. Hardwood trees > 40 cm (> 16 in) dbh, and > 18 m (> 59 ft) tall in uplands or > 24 m (> 79 ft) tall in bottomlands. 2. Closed canopy hardwood forest. 3. Dead, mature, canopy height deciduous trees may be present. 4. Less than 20% conifers by basal area.

Table 2. Map accuracy error matrix of field-checked sites for a GIS-based potential habitat map for Henslow's sparrow (*Ammodramus henslowii*) at Fort Knox, KY, USA, 1996.

	Actual			
Predicted	Not Habitat	Habitat	Total	Producer's Accuracy (%)
Not Habitat	128	3	131	97.7
Habitat	9	2	11	18.2
Total	137	5	142	
User's Accuracy (%)	93.4	40.0		91.6

Table 3. Map accuracy error matrix of field-checked sites for a GIS-based potential habitat map for cerulean warbler (*Dendroica cerulea*) at Fort Knox, KY, USA, 1996.

	Actual			
Predicted	Not Habitat	Habitat	Total	Producer's Accuracy (%)
Not Habitat	116	3	119	97.5
Habitat	21	2	23	8.7
Total	137	5	142	
User's Accuracy (%)	84.7	40.0		83.1

Table 4. Map accuracy error matrix of field-checked sites for a GIS-based potential habitat map for cedar barrens at Fort Knox, KY, USA, 1996.

	Actual			
Predicted	Not Habitat	Habitat	Total	Producer's Accuracy (%)
Not Habitat	123	0	123	100.0
Habitat	18	1	19	5.2
Total	141	1	142	
User's Accuracy (%)	87.2	100.0		87.3

FIGURE LEGENDS

Figure 1. Inductive method for developing a land use/land cover map for Fort Knox, KY, USA combining Land Condition Trend Analysis (LCTA) field data and a Landsat Thematic Mapper satellite image. The final Land Cover Map can be seen on the Web at http://www.esd.ornl.gov/programs/SERDP/knox92.gif.

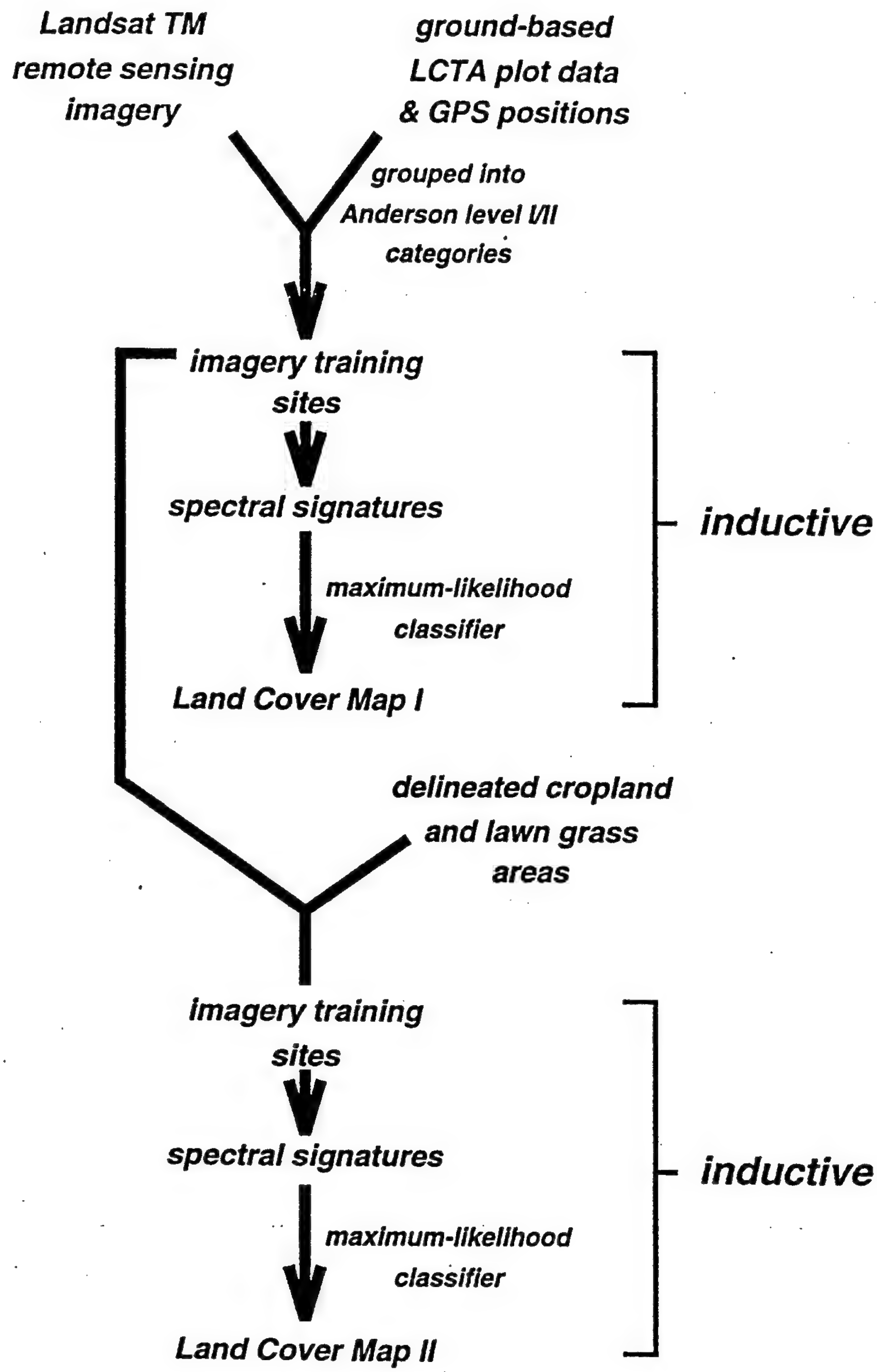
Figure 2. Development flowcharts for predicting potential Cedar Barrens and ideal training areas for treaded or tracked armored vehicles (Tank movement/training areas). While the tank movement areas methods rely solely on deductive inference of a set of rules, the cedar barrens habitat prediction is a combination of *a priori* rules and field occurrence data within a smaller preserve.

Figure 3. Comparison of predicted potential cedar barrens habitat (above) and actual barrens mapped within the Cedar Creek Glades Preserve area (below, from White et al. 1994) at Fort Knox. One km grid lines in both maps can be used for relative location reference. Nearly every actual barren in the lower map is predicted by the cedar barren habitat model. Southern extreme of Preserve is the southern boundary of the Fort Knox reservation.

Figure 4. Combination deductive/inductive method used to predict potential habitat for Henslow's sparrow (*Ammodramus henslowii*), based on habitat specification rules and a ground-based nesting location.

Figure 5. Predicted maps of potential Cedar Barrens habitat and Henslow's sparrow (*Ammodramus henslowii*) nesting habitat within the Fort Knox military Reservation, KY, USA. Black areas indicate predicted or potential habitat. Roads are shown in gray for orientation. Coordinates are Universal Transverse Mercator (UTM) meters, Zone 16, North American Datum 1927, divided by 1000; grid lines are 5 km apart.

Figure 6. Predicted maps of ideal training areas for treaded or tracked armored vehicles (Tank movement/training areas) and potential Cerulean warbler (*Dendroica cerulea*) habitat within the Fort Knox military Reservation, KY, USA. Black areas indicate predicted or potential habitat. Roads are shown in gray for orientation. Coordinates are Universal Transverse Mercator meters, Zone 16, North American Datum 1927, divided by 1000; grid lines are 5 km apart.


Landsat TM
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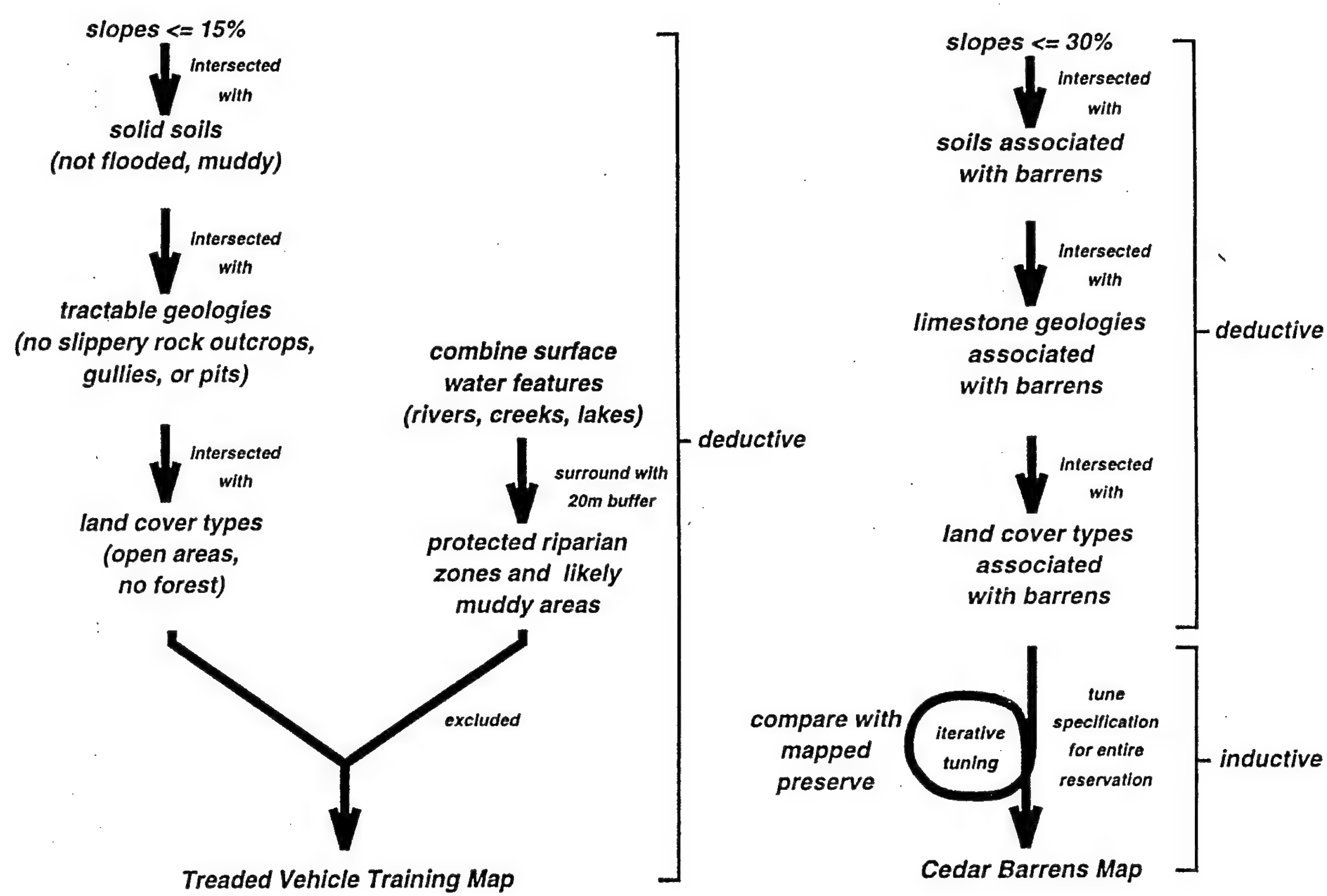
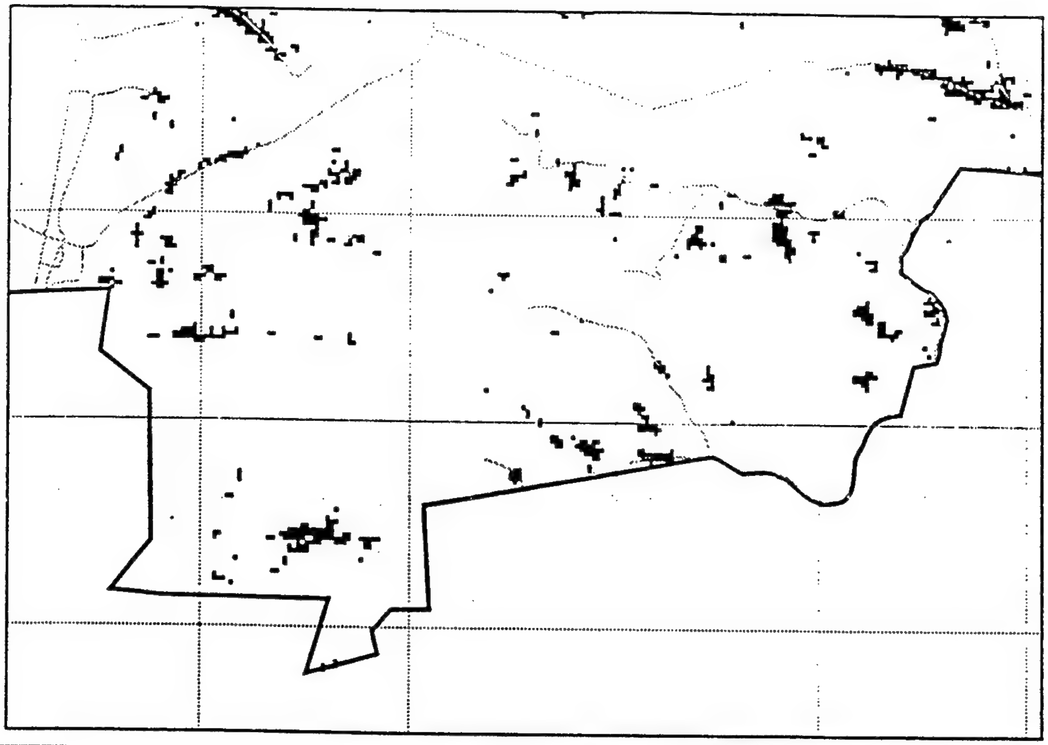
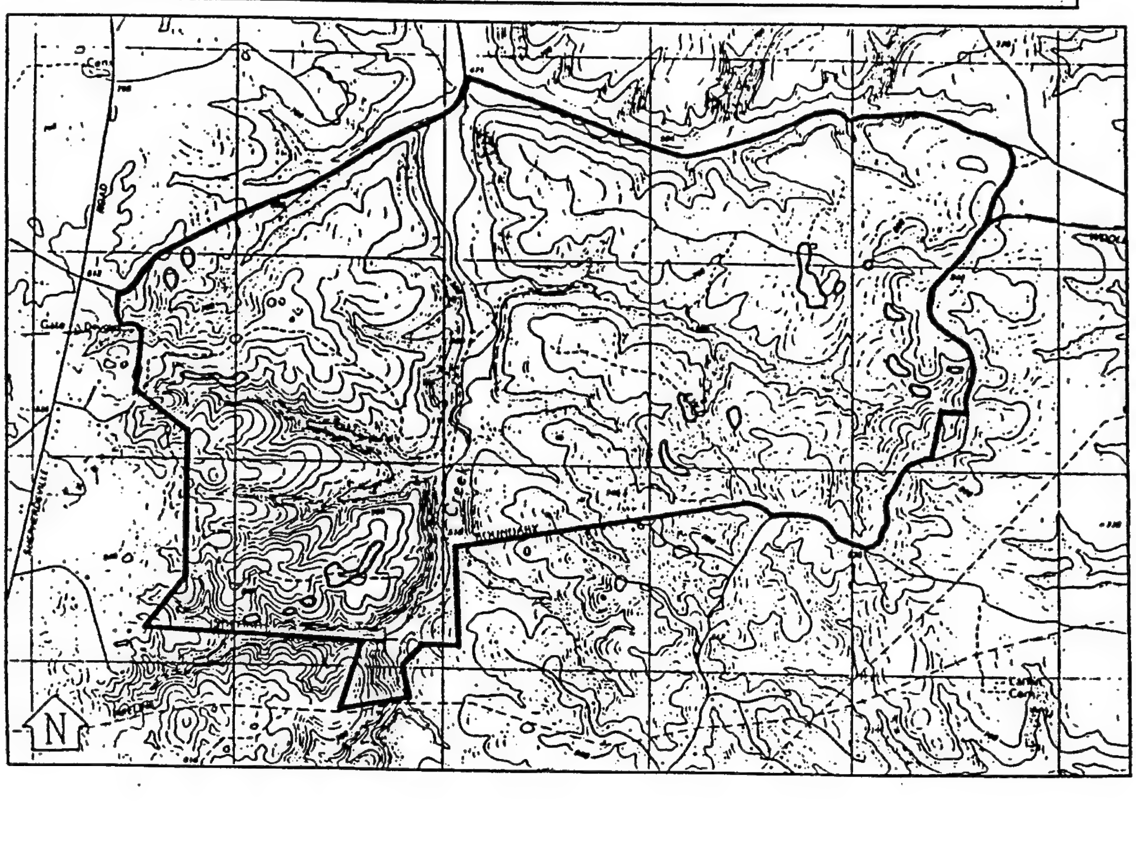


slopes <= 15%
intersected with
solid soils (not flooded, muddy)
intersected with
tractable geologies (no slippery rock outcrops, gullies, or pits)
intersected with
land cover types (open areas, no forest)
combine surface water features (rivers, creeks, lakes)
surround with 20m buffer
protected riparian zones and likely muddy areas
excluded
Treaded Vehicle Training Map
deductive
slopes <= 30%
intersected with
soils associated with barrens
intersected with
limestone geologies associated with barrens
intersected with
land cover types associated with barrens
deductive
compare with mapped preserve
iterative tuning
tune specification for entire reservation
inductive
Cedar Barrens Map

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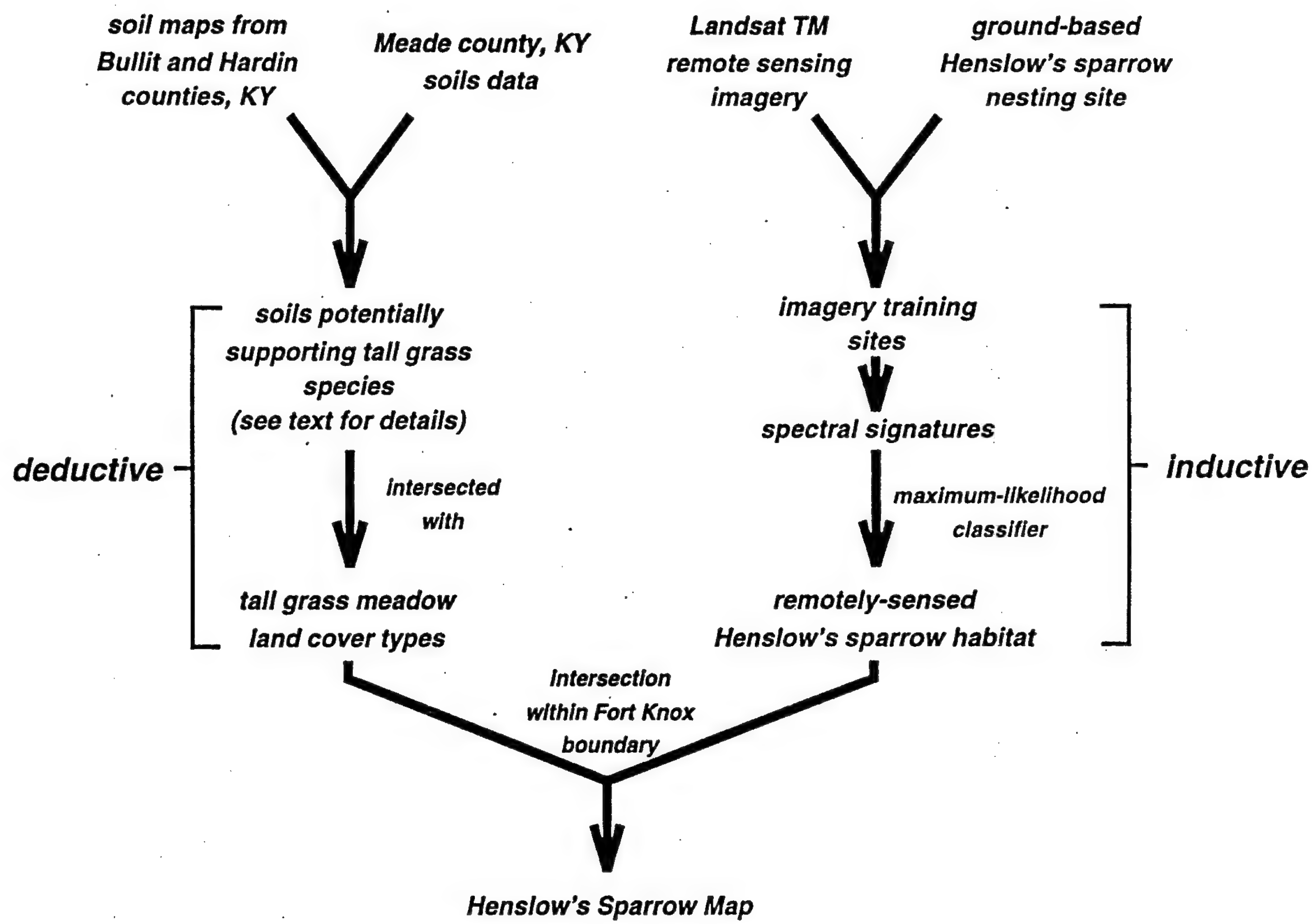
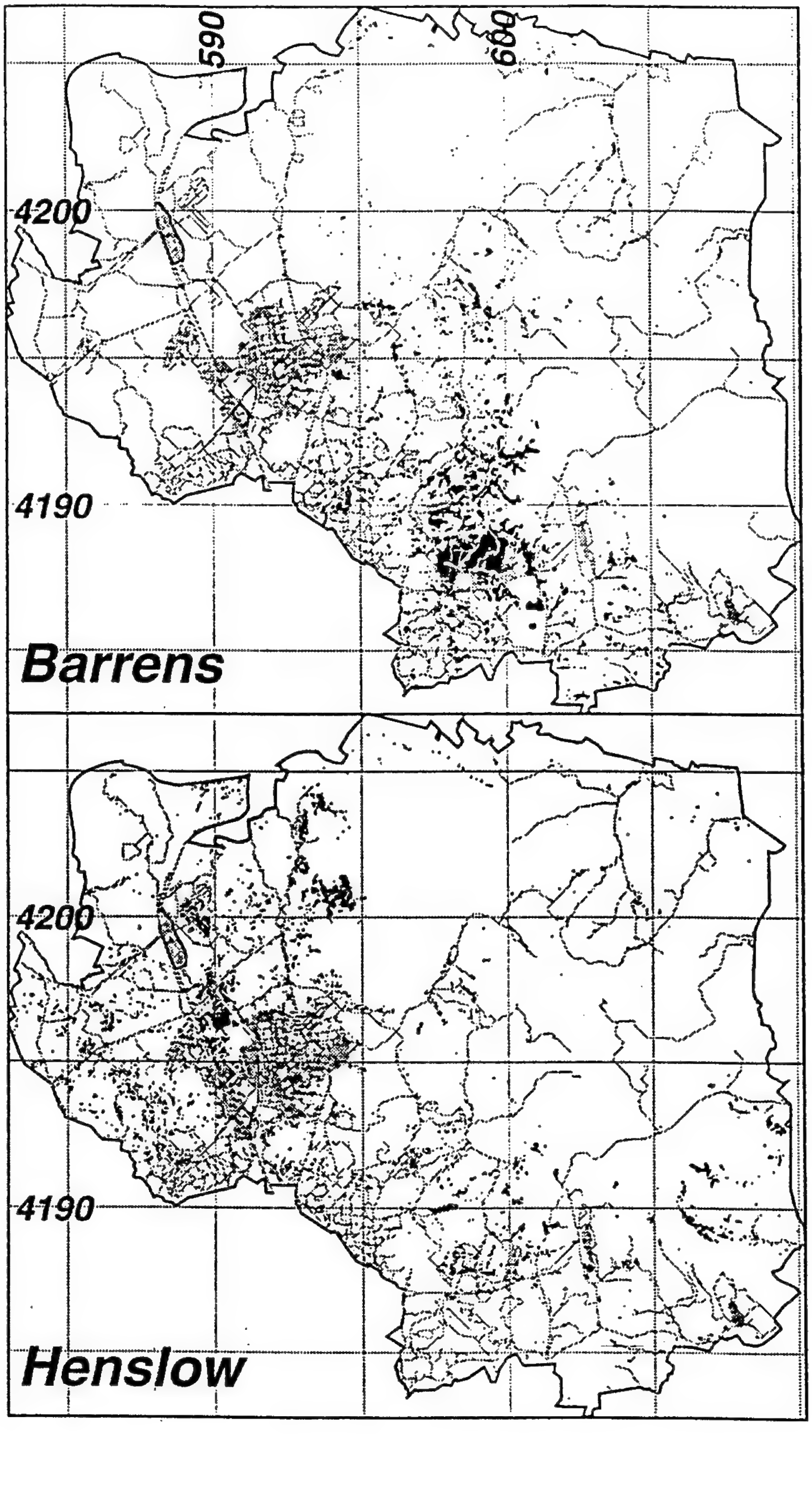

soil maps from Bullit and Hardin counties, KY
Meade county, KY soils data
Landsat TM remote sensing imagery
ground-based Henslow's sparrow nesting site
soils potentially supporting tall grass species (see text for details)
imagery training sites
spectral signatures
deductive
intersected with
maximum-likelihood classifier
inductive
tall grass meadow land cover types
remotely-sensed Henslow's sparrow habitat
Intersection within Fort Knox boundary
Henslow's Sparrow Map


590
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Barrens
4200
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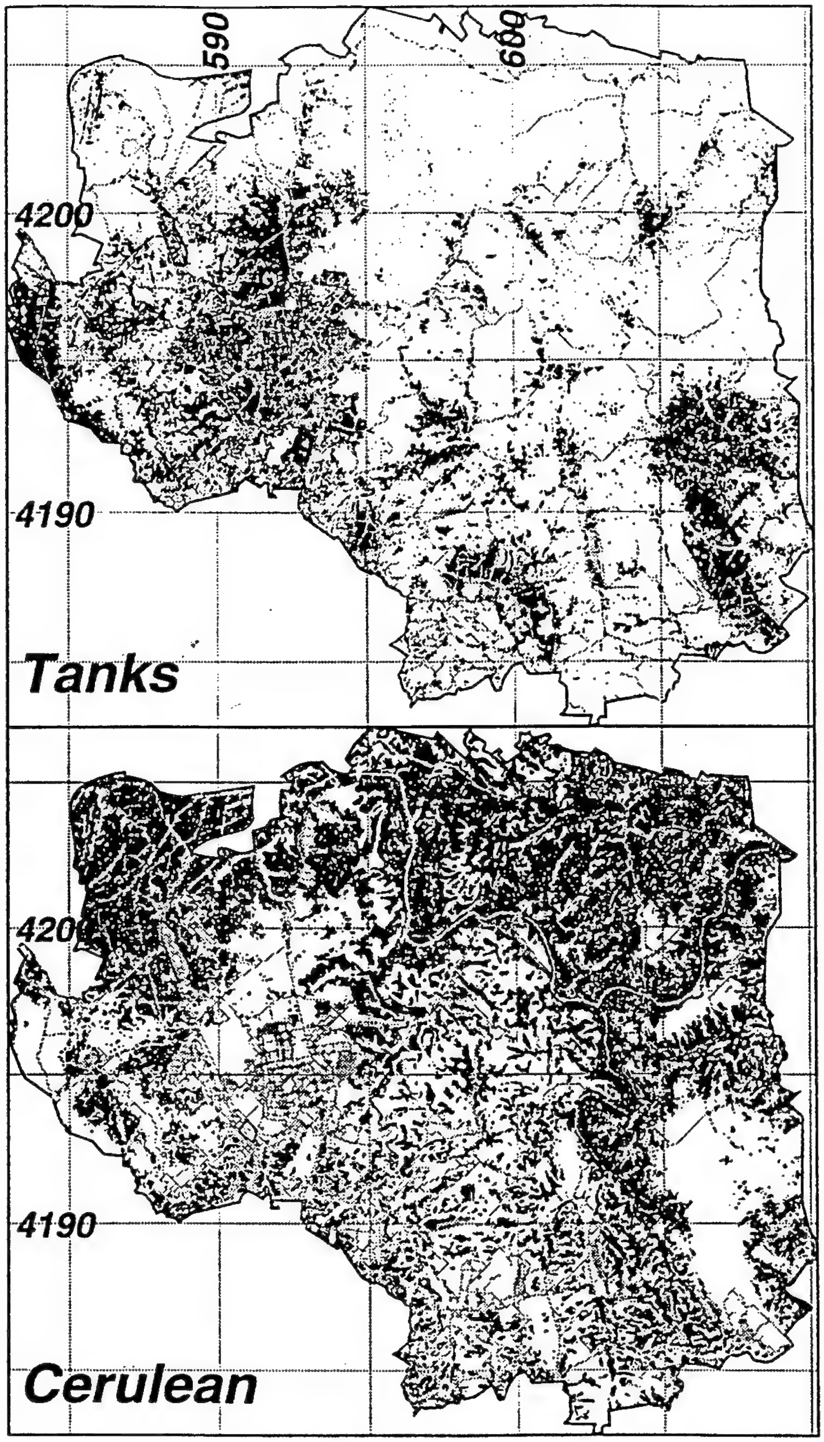
Henslow


590
600
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4190
Tanks
4200
4190
Cerulean

Assessing the Persistence of an Avian Population in a Managed Landscape: A Case Study With Henslow's Sparrow at Fort Knox, Kentucky*

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Abstract

We describe a model of how the spatial distribution of nesting habitat affects the reproductive success of territorial migrant bird species breeding in fragmented landscapes. The model combines a landscape perspective with conventional avian demographic modeling to provide a tool for the assessment of how land-use change might impact the persistence of avian populations. Nesting habitat is mapped with a reqular grid of square cells. Neighboring cells are aggregated to form patches. Territories are distributed among patches using logistic regressions describing the relationship between species' occurrence and patch area. Nesting success in each patch is a function of the patches edge:area ratio, reflecting the association of edge with increased risk of predation and brood parasitism. The number of female fledglings produced by all patches is used to calculate the expected number of female fledglings per female. This demographic variable, an explicit consequence of landscape structure, is combined with survivorship in a life-table model to calculate the demographic indices of net lifetime maternity and the finite rate of increase. These indices provide a simple characterization of the landscape as a population source or sink. We describe an implementation of the model for Henslow's Sparrow (*Ammodramus henslowii*) at the Fort Knox Military Reservation, Fort Knox, Kentucky. The model indicates that the Fort Knox landscape is a population sink for Henslow's Sparrow, with an annual rate of decline of approximately 22%. Analysis of the model results suggest that the prediction of a declining population at Fort Knox is a consequence of too little successful reproduction combined with too low a rate of juvenile survivorship.

Introduction

Loss of habitat and fragmentation of the remaining habitat have been implicated in the decline of many bird populations in North America and elsewhere (Whitcomb et al. 1981; Wilcove et al. 1986; van Dorpe & Opdam 1987; Enoksson et al. 1995; Robinson et al. 1995; Stouffer & Bierregaard 1995). Neotropical migrants and forest-interior species are often the focus of these concerns, but shorter distance migrants, residents, and grassland species may also be impacted (Herkert 1994; Enoksson et al. 1995). Deforestation, urbanization, and the conversion of native grasslands to pasture and cropland reduce the availability of suitable habitat. The increase in edge habitat that accompanies fragmentation may increase brood parasitism and nest predation and lower reproductive success (Paton 1994). Isolation and insularization (Wilcox 1980) can interfere with dispersal and contribute to the decline and extinction of local populations. Fragmented landscapes may function as population sinks where reproduction fails to compensate for mortality (Pulliam 1988; Pulliam & Danielson 1991; Robinson 1992; Donovan et al. 1995). Persistence of a species in these sink landscapes requires immigration of individuals from more productive source landscapes. Pulliam (1988) introduced the concept of demographic source-sink with reference to "habitat", or more generally "compartment", but the idea is easily extended to a heterogeneous spatial extent or landscape composed of multiple habitat types (Donovan et al. 1995).

Assessing the persistence of avian populations in fragmented landscapes requires an explicit consideration of the effects of spatial structure and landscape pattern on population dynamics. Compliance with directives for ecosystem management and preservation of biodiversity on public lands (Cooperrider 1991; Salwasser 1991; Petit et al. 1995; Beattie 1996;

Dombeck 1996; Goodman 1996; Thomas 1996) will require assessment of how landscape pattern and changes in landscape pattern affect bird populations. Land managers need to know whether the landscapes under their purview are functioning as sources or sinks for species of conservation concern, and whether feasible changes in land use and the resulting landscape pattern could shift a landscape from sink to source.

Here we describe a model of spatially structured avian demography. The model combines a landscape perspective with demographic modeling to provide a tool for the assessment of land use and land-use change on the persistence of bird populations in a managed landscape. The version of the model described here applies to territorial migrants. The model assumes that landscape structure only affects female fecundity on the breeding ground. Survivorship is not affected, and the migration and overwintering stages of the annual life cycle are not modeled. Designed explicitly as an assessment tool, the model strives for simplicity and ease of implementation. Accordingly, the model is primarily phenomenological in nature and does not attempt a mechanistic description of avian biology. Model inputs and, just as importantly, the data required to test the model are parameters and variables that can be taken from existing literature, or can reasonably be expected to be collected as part of a landscape assessment.

The model was specifically developed for the assessment of avian demography on Department of Defense (DoD) installations, and we present a case study here of Henslow's Sparrow (*Ammodramus henslowii*) at the Fort Knox Military Reservation, Fort Knox, Kentucky. However, the model's general structure also applies to other territorial migrants on other landscapes, both public and private.

The Model

Consider a landscape of several thousand hectares in the breeding range of a migratory bird species. The species is monogamous on the breeding grounds, and mated pairs establish and defend all-inclusive Type A territories within which nesting and most foraging takes place (Hinde 1956; Morse 1980). The landscape is mapped with a regular grid of square cells. Habitat used for nesting is distinguished from non-nesting habitat. Cells of nesting habitat separated by less than the distance the pair will readily cross in using and defending their territory, their gap-crossing ability (Dale et al. 1994), are aggregated into patches. Vegetation or landcover within a patch is perceived as contiguous homogeneous nesting habitat. The matrix between patches is not used for nesting.

Patches of nesting habitat smaller than the species' territory size are not used for nesting. Patches larger than this minimum size are filled with territories (equivalently: nests, breeding pairs, or breeding females) according to an incidence function $J(A)$ (Wilcove et al. 1986) which describes the probability of encountering a breeding pair (or territory) at a random point in a patch of area A (Robbins et al. 1989) (Fig. 1). Incidence is calculated with a logistic regression model

$$J_A = \frac{\exp[\beta_0 + \beta_1 \log_{10} A + \beta_2(\log_{10} A)^2]}{1 + \exp[\beta_0 + \beta_1 \log_{10} A + \beta_2(\log_{10} A)^2]} \tag{1}$$

where β_0, β_1 and β_2 are model (regression) parameters. The probability of occurrence J_A is interpreted as the proportion of the patch occupied, and the number of nests $\mathcal{N}$ in patch i is the occupied area divided by territory size, or

$$\mathcal{N}_i = J_A A_i / A_T \tag{2}$$

where A_T is territory size (ha), and $\mathcal{N}_i$ is rounded to the nearest integer. The maximum number of nests in a patch is patch area divided by territory size and occurs when $J_A = 1.0$.

Each nest in each patch produces a clutch of eggs. Clutch size C for each nest is drawn independently from a species- or population-specific frequency distribution. The clutch size of some species is uniformly distributed between a minimum and maximum; others have a model clutch size. Consequently, clutch size may vary among nests.

Nesting success, the probability that a nest will produce at least one fledgling (Johnson & Temple 1986), is a function of a patch's edge:area ratio. Reflecting the assumption that higher rates of nest predation and parasitism are associated with increased amounts of edge, and edge has a negative affect on nesting success, nesting success is lower in patches with a large edge:area ratio (i.e., those patches with lots of edge per unit area). Maximum nest success occurs in large patches with relatively little edge. The edge:area ratio is normalized by the edge:area ratio of a single square cell, yielding an edge:area index with a maximum value of 1.0 indicating maximum edge per unit area. A value near 0.0 indicates a patch with minimal edge per unit area. The probability of nesting success in patch i, S_i, is given by

$$S_i = S_{\max} \frac{1}{1 + (e_i/k)^{\theta}} \tag{3}$$

where $S_{\max}$ is the maximum probability of nesting success for patches with an edge:area ratio approaching zero, or, equivalently, nesting success in the absence of any edge effect,

and e_i is the normalized edge:area index of patch i. The parameter k is the value of e_i where $S_i = 0.5S_{\text{max}}$, and θ is a parameter which determines the rate at which nesting success declines with larger edge:area ratios.

Nesting success in the absence of any edge effect, S_{max}, will be less than one; some nests will be loss to predation, storms, or other factors, regardless of their proximity to an edge. The probability of nesting success will be less than one even in the largest most contiguous patch of habitat. Some species will be relatively insensitive to edge, at least until patches become mostly edge (i.e., the edge:area index approaches 1). We refer to this pattern as a Type I edge response (Fig. 2). Other species will be very sensitive to edge, and the probability of nesting success will decline very rapidly with an increasing edge:area ratio (a Type III response, Fig. 2). Others will show an intermediate response of more gradual decline with increasing edge per unit area (Type II, Fig. 2) Calibration of the parameters S_{max}, k, and θ will fit the nesting success curve of Eq. 3 to any observed or hypothesized response to edge within this family of response curves.

Nesting success in the model is evaluated stochastically for each nest in a patch. The probability that a nest in patch i fledges no young is $1 - S_i$. Nests which fledge at least one young are assumed to fledge the entire clutch, so F_{ji}, the number of fledglings from nest j in patch i, is C_{ji} (the clutch size of that nest) for successful nests and 0.0 for unsuccessful nests.

The sex of each fledgling is determined stochastically according to the population's fledgling female:male sex ratio. Thus, it is possible for a nest to produce only male or only female fledglings, but cumulatively, across all nests in the landscape, the ratio of female

to male fledglings will approach the population's or species' fledgling sex ratio (normally assumed to be 1:1 or 50% females).

Productivity, the number of fledglings (of both sexes) per nest (or territory or pair) for patch i, is

$$P_i = \frac{\sum_{j=1}^{\mathcal{N}_i} F_{ji}}{\mathcal{N}_i} \tag{4}$$

where F_{ji} is the number of fledglings in nest j of patch i. Productivity can vary from patch to patch, primarily as a consequence of patch variability in the probability of nesting success, itself a consequence of variability in edge:area among patches. Thus the model reflects variability in patch "quality" and contribution to population dynamics (Pulliam & Danielson 1991) but only that associated with patch size and shape. Productivity for the entire landscape or population, P_L, (not the mean of patch productivity) is

$$P_L = \frac{\sum_{i=1}^{m} \sum_{j=1}^{\mathcal{N}_i} F_{ji}}{\sum_{i=1}^{m} \mathcal{N}_i} \tag{5}$$

where m is the number of patches. Note that these estimates of productivity incorporate reductions in productivity due to nest failure. The expected productivity of successful pairs (or nests) is the mean clutch size.

The demographic parameter b, the expected number of female fledglings produced per female, is

$$b = \frac{\sum_{i=1}^{m} \sum_{j=1}^{\mathcal{N}_i} F_{ji}^{\gamma}}{N_a} \tag{6}$$

where F_{ji}^{γ} is the number of female fledglings in nest j of patch i (the γ distinguishes the number of female fledglings from the number of fledglings of either sex in Eqs. 4 and 5),

and N_a is the total number of adult reproductive females in the landscape population. In determining b, the model assumes that the number of adult females is equivalent to number of territories (i.e., nests or mated pairs) so $N_a = \sum_{i=1}^{m} \mathcal{N}_i$. Note that this assumption results in a maximum value for b for a landscape with nesting habitat fully occupied by mated pairs. The presence of non-mated non-nesting females would reduce b.

The model assumes productivity is independent of age after sexual maturity. The maternity function m_x, the number of female fledlings produced by a female of age x, is then $m_x = b$ for all ages x.

The maternity function is combined with age-specific survivorship to create a life table for the landscape's population (Leslie 1966; Mertz 1971; Nichols et al. 1980; Lande 1988; Noon & Biles 1990) (Table 1). Annual survival probabilities are defined for three age classes: juveniles s_0, subadults s_1, and adults s.

Two demographic indices are calculated from the life table. The first is net lifetime maternity or net reproductive rate:

$$R_0 = \sum l_x m_x \tag{7}$$

where R_0 is the expected lifetime production of females by a female fledgling, and l_x is the probability of survivorship to age x from the life history table. For a stable age distribution, when $R_0 = 1.0$, a female replaces herself in her lifetime, and the population is stable. If $R_0 < 1.0$ the population is declining, and if $R_0 > 1.0$ the population is increasing.

The second demographic index is the finite rate of increase λ given by the solution of the

Table 1. Life history table.

x^a	$l_x{}^b$	$m_x{}^c$	$l_x m_x{}^d$
0	1.0	0	0
1	s_0	b	$s_0 b$
2	$s_0 s_1$	b	$s_0 s_1 b$
3	$s_0 s_1 s$	b	$s_0 s_1 bs$
4	$s_0 s_1 s^2$	b	$s_0 s_1 bs^2$
.	.	.	.
.	.	.	.
.	.	.	.
x	$s_0 s_1 s^{x-2}$	b	$s_0 s_1 bs^{x-2}$

[a]age in years
[b]probability of survivorship to age x
[c]female fledglings per female aged x
[d]net maternity function

characteristic equation (Noon & Biles 1990):

$$\lambda^T - s\lambda^{T-1} - bs_0s_1s^{T-2} = 0 \tag{8}$$

where $T \geq 1$ is the age of sexual maturity and $0 < s < 1$. If $\lambda = 1.0$ the population is stable. When $\lambda < 1.0$ the population is declining, and if $\lambda > 1.0$ the population is increasing. The annual rate of change of the population size (% yr^{-1}) is $(\lambda - 1.0) \times 100$.

In addition, the life table parameterizes an age classified matrix population model (Caswell 1989). This Leslie matrix is used to project population numbers forward in time.

The Landscape

Fort Knox Military Reservation, Fort Knox, Kentucky (hereafter referred to simply as Fort Knox) occupies 44,150 ha of Bullitt, Hardin, and Meade counties in north central Kentucky (Figure). Bordered on the north by the Ohio River, Fort Knox is drained by Otter Creek and by the Salt River and its tributary, the Rolling Fork. Muldraugh's Hill, a steep escarpment, runs northwest to southeast through Fort Knox and roughly divides the Reservation into a hilly eastern portion dominated by the Salt River-Rolling Fork watershed and a western karst plateau of rolling uplands and numerous sinkholes (White et al. 1994).

Most of the reservation is covered by second-growth deciduous forest (Fig. 4). Mesophytic forest is found in the lower ravines and in the floodplains of the smaller rivers and creeks. Swamp or bottomland hardwood forest can be found in the larger floodplains, especially adjacent to the Ohio River. Sub-xeric forest occupies the higher ridgetops and is predominant

in the southern part of Fort Knox. This part of the Reservation is also characterized by the presence of several large limestone slope glades (White et al. 1994). The western uplands of Fort Knox are heavily impacted by human occupation and military training activities. The barren areas on the western edge of Fort Knox (Fig. 4) are largely areas stripped of vegetation by tank and other tracked vehicle traffic. This portion of Fort Knox lies in the northern Elizabethtown Subsection of the Pennyroyal Plain Subsection of the Highland Rim, and historically was considered part of the "Big Barrens" a grass-dominated prairie landscape (Quarterman & Powell 1978; DeSelm & Murdock 1993; White et al. 1994). This region is now heavily disturbed, but representatives of the former prairie or grassland flora can still be found in small scattered fragments throughout this portion of Fort Knox. Croplands and pastures dominate the landscape west of the Fort Knox boundary (Fig. 4).

The Species

Henslow's Sparrow (*Ammodramus henslowii*) is a small grassland species associated with dense, tall grasslands (including hay fields) which are not mowed or burned annually (Skinner et al. 1984; Zimmerman 1988; Rising 1996). Henslow's Sparrow breeds in the north central-eastern United States from South Dakota (east of the Missourii River) and eastern Kansas to New York, Virginia and eastern or coastal North Carolina. The northern limit of its range is in central Minnesota, Upper-Peninsular Michigan, and southern Ontario (Beyers et al. 1995; Rising 1996). Northern Kentucky and Fort Knox are on the southern edge of the species' breeding range, and Rising (1996) indicates their occurrence in central and western Kentucky is irregular. Listed by the Kentucky State Nature Preserves Commission as a

species of Special Concern (KSNPC 1993), the largest documented summer population in Kentucky is found at Fort Knox where grasslands in the vicinity of Godman Army Airfield are managed as a protected area for Henslow's Sparrow (White et al. 1994). A short to medium distance migrant, the species winters in the coastal plain of the southeastern United States.

Historically, populations of Henslow's Sparrow west of the Appalachians were probably most associated with native tall grass prairies, forest prairie mosaic, and moist grasslands in forest openings (Graber 1968; Zimmerman 1988). The species' gradual but persistent decline has been attributed to decreasing availability of suitable habitat, primarily standing dead vegetation in open grassland (Zimmerman 1988). It is currently thought to be habitat limited because grasslands used by people are usually harvested or burned annually (if not more frequently) (Zimmerman 1988), and in the eastern portions of its range, abandoned fields are relatively rapidly invaded by shrubs and trees. Too frequent burning (e.g., annual) removes the standing dead grass cover preferred by Henslow's Sparrow, but the complete suppression of less frequent fires allows the growth of woody vegetation that the species' tends to avoid (Zimmerman 1988). This species is also area sensitive, preferring patch sizes of 30 ha or more (Zimmerman 1988; Herkert 1994).

The dense grass preferred by the birds will only be produced on relatively productive sites with adequate moisture (Robins 1971b; Abrams et al. 1986; Zimmerman 1988; Heikens & Robertson 1995). Native tall grass prairie meets the habitat requirements of Henslow's Sparrow, if it isn't burned every year. In Missouri, for example, Henslow's Sparrow occurs only on idle or lightly grazed, unburned prairie (Skinner et al. 1984). The sparrow does

not usually nest in sites that are either too wet or too dry, and it prefers sites with little or no woody vegetation (Zimmerman 1988; Hamel 1992). Some of the literature describes fairly wet sites (e.g., of cordgrass, *Spartina pectinata* (Hyde 1939)) where Henslow's Sparrow has been observed nesting, but it is more commonly reported in more typical prairie-like grassland habitat (Graber 1968; Wiens 1969; Zimmerman 1988; Herkert 1994). Management recommendations are for a fire management rotation of burning every three to four years to eliminate woody vegetation (Zimmerman 1988). The resulting suitable habitat should contain no more than about 1 sapling per 100 m^2 (personal communication, Ken Palmerball, Kentucky Nature Preserves Commission, April, 1996).

Because Henslow's Sparrow is a species of conservation concern at Fort Knox (White et al. 1994), and because the nesting habitat of Henslow's Sparrow is potentially vulnerable to tank training activities, we chose to implement the model described above for the Henslow's Sparrow population of the Fort Knox landscape. This implementation is best considered an example or case study of the model's implementation and use, rather than an analysis of Henslow's Sparrow demography *per se*.

A Habitat Model

As noted above, a summer population of Henslow's Sparrow is known from the Godman Army Airfield at Fort Knox. The presence of singing males suggests that this is a breeding population (White et al. 1994). However, the presence of Henslow's Sparrow elsewhere at Fort Knox is not documented, and a map of nesting habitat (one of the model requirements) was not available. Accordingly, we developed a model of Henslow's Sparrow nesting habi-

tat to describe the expected spatial distribution of nesting habitat across the Fort Knox landscape.

Details of this habitat model can be found in Hargrove et al. (submitted). Briefly, for our purpose here, our prediction of Henslow's Sparrow habitat at Fort Knox is based on identifying 1) sites which were probably prairie prior to extensive agricultural conversion, 2) sites which probably could support prairie or dense grass vegetation, and 3) sites which would be unlikely to support prairie or dense grass vegetation. We assume Henslow's Sparrow does not nest in areas frequently flooded or with standing water, but might nest in seasonally wet areas. We also assume that it does not nest in areas too dry or infertile to produce dense grass. Our approach was to combine information from the literature with readily available soil survey interpretations from published Hardin and Bullitt County Soil Surveys (Arms et al. 1979; USDA/SCS 1986) and the draft unpublished Meade County Soil Survey.

Sites which were probably originally prairie are those with soils that are Mollisols. Related soils at Fort Knox that show some properties of Mollisols are mollic Hapludalfs and mollic Paleudalfs (types of Alfisols). These soils probably developed under cane or prairie vegetation or show characteristics transitional to prairie soils (Arms et al. 1979).

Although not under continuous grass or herbaceous vegetation for thousands of years, other soil types at Fort Knox might have also have been prairie vegetation. Soils classified as Alfisols are thought to have developed primarily under forest vegetation, but could also have supported prairie vegetation for periods of time, especially in the prairie transition region in the vicinity of Fort Knox. Many of the Alfisols at Fort Knox are deep and well drained and would support dense grasslands suitable for Henslow's Sparrow habitat. Some Alfisols

(Aqualfs and Fragiudalfs) have a perched water table less than 3 ft (.91 m) below the surface, but most of these soils are probably dry enough to support wet prairie grasses.

Other soils at Fort Knox which are unlikely to support prairie or dense grass suitable for Henslow's Sparrow habitat are too wet, too dry, or unproductive. Aquolls, some of the Alfisols, some of the Inceptisols, and some of the Entisols at Fort Knox have the water table less than one foot below the surface or are frequently flooded; these soils are assumed to be too wet for preferred Henslow's Sparrow habitat. Heikens and Robertson (1995) found that soils deeper than 40 inches (1 m) were most likely to support prairies in the loess hills of southern Illinois, while shallower soils were likely to support sparsely vegetated 'glade' vegetation. Therefore, soils less than 1 meter deep at Fort Knox are assumed to be too dry to support the dense vegetation necessary for Henslow's Sparrow habitat. Similarly, coarse textured, severely eroded, steep, or gullied land (some Alfisols, Entisols, and Inceptisols), and older, leached soils, developed under forest (Ultisols) would probably not have adequate fertility or moisture to support dense grassland vegetation under natural conditions, and they were not included in our model of Henslow's sparrow habitat.

Map layers for soils and vegetation land cover (Fig. 4) were combined in a raster Geographical Information System (GIS). Soils identified as potentially suitable to support prairie or dense stands of grass (Table 2) were then compared with land cover. Pixels of either unsuitable soil types (Table 2) or unsuitable land cover (Table 3) were then eliminated as unsuitable as potential Henslow's Sparrow habitat.

To further refine our prediction of Henslow's Sparrow habitat, a 100 m radius circle enclosing the known nesting habitat at Fort Knox's Godman Army AirField (White et al.

1994) was used to identify areas with similar spectral characteristics elsewhere at Fort Knox (Hargrove et al., submitted). A maximum likelihood classification was run with the spectral signature for the known habitat and raw Landsat TM spectral data for Fort Knox (Hargrove et al., submitted), and a Chi-square test applied to each discriminant result at every cell. The resulting reject threshold map contained the confidence level at which each cell in the map was classified. Cells with $< 5\%$ probability of being correctly assigned to the Henslow's Sparrow habitat class were defined as not suitable for Henslow's Sparrow habitat. A spectral signature was developed for these non-habitat cells, and the maximum likelihood classification repeated to produce a binary habitat-nonhabitat prediction. The intersection of the soil-landcover prediction and the spectral signature prediction of habitat was taken as our prediction of Henslow's Sparrow habitat (i.e., cells predicted to be habitat by both methods were defined as nesting habitat).

The resulting map of potential Henslow's Sparrow nesting habitat is shown in Figure 5. Characterization of the map's accuracy can be found in (Hargrove et al., submitted).

Life History Parameters

The model's life history parameters for Henslow's Sparrow are shown in Table 4. Ideally these parameters would be population specific (i.e., estimated from observations and measurements of Henslow's Sparrow at Fort Knox). Those data are not available. We therefore assume that our species-specific estimates for territory and clutch size derived from literature on Henslow's Sparrow at other sites (Hyde 1939; Graber 1968; Wiens 1969; Robins 1971a; Robins 1971b; Beyers et al. 1995; Rising 1996) apply to the population at Fort Knox. Similarly, we used

Table 2. Suitability of soils at Fort Knox for supporting Henslow's Sparrow habitat.

Soil taxonomic group	Suitable	Unsuitable
Mollisols	Typic Argiudolls	Aquolls (too wet)
		Lithic Argiudolls, lithic Hapludolls, and other shallow Hapludolls (too shallow to bedrock)
Alfisols	Paleudalfs and mollic Hapludalfs	Lithic and some typic and ultic Hapludalfs (too shallow to bedrock)
	Some typic and ultic Hapludalfs (> 40 inches (1 m) to bedrock)	Severely eroded phases of all soils (too droughty or infertile)
	Fragiudalfs (perched water table > 1 foot (0.3 m) below the surface)	Aqualfs with water table < 1 foot below the surface (too wet)
Ultisols	Some Hapludults (> 40 inches (1 m) to bedrock)	Some Hapludults (too shallow to bedrock)
		Severely eroded phases of all soils (too droughty or infertile)
Inceptisols	Most Eutrochrepts	Dystric Eutrochrepts and lithic Dystrochrepts (too shallow to bedrock)
		Fluventic Eutrochrepts (frequently flooded - too wet)
Entisols	None	Gullied Udorthents (too unproductive)
		Fluvaquents and Udipsamments which are frequently flooded or with water table < 1 foot (0.3 m) below the surface (too wet)

Table 3. Suitability of landcover types at Fort Knox for supporting Henslow's Sparrow habitat.

Landcover type	Suitable	Unsuitable
Deciduous forest		X
Mixed forest		X
Evergreen		X
Transitional	X	
Barren	X	
Urban		X
Water		X
Maintained grass	X	
Cropland	X	
Lawn Grass		X

the incidence function for Henslow's Sparrow from Herkert's (1994) study of grassland bird communities in Illinois (Fig. 1).

Lacking information on survivorship for Henslow's Sparrow, we estimated juvenile and adult survivorship from the life table data of the Baker et al. (1981) study of White-Crowned Sparrows (*Zonotrichia leucophrys nuttalli*) in California. These estimates may be too high. The White-Crowned Sparrow population of Baker et al. (1981) is nonmigratory, and Henslow's Sparrow is about half as massive as the White-Crowned Sparrow (Rising 1996) (survivorship is positively correlated with body mass). Nevertheless, these estimates are consistent with the range of survivorship reported for small passerines (Ricklefs 1992).

We assumed first reproduction at an age of 1 yr. We estimated life expectancy (Table 4) from the allometric equation of Lindstedt & Calder (1976): $L = 17.6M^{0.20}$, where L is longevity (yr), and M is body mass (kg). We assumed a mass for Henslow's Sparrow of 13 g (Rising 1996).

Johnson & Temple (1986) reported fairly low probabilities of nesting success (24–56%) for ground nesting passerines in fragmented tallgrass prairies of western Minnesota, even when nests were far (> 45 m) from a forest edge. We therefore assumed our Type III response to edge for Henslow's Sparrow (Fig. 2). Assuming a square patch (Johnson & Temple 1990 describe the patches as compact) we estimated the edge:area index e_i for both their large (130–486 ha, $e_i = 0.0091 - 0.0175$) and small (16–32 ha, $e_i = 0.0357 - 0.05$) patches. We used the higher Johnson & Temple (1986) estimates of nesting success (those from recently burned plots) far from an edge to estimate nesting success for Henslow's Sparrow for patches with minimal edge, i.e., those with an edge:area index near 0.0 (Fig. 6). We assumed that

the rates of nesting success near to an edge reported by Johnson & Temple (1986) applied to linear patches with edge:area indices ranging from 0.2 - 0.5. Here we also used the highest values from better quality, recently burned, patches (Fig. 6). We assumed a nesting success of 80% in the absence of any edge effect ($S_i = S_{\max} = 0.80$ when $e_i = 0.0$). Arcese et al. (1992) report a minimum nest failure rate of approximately 20% for a Song Sparrow (*Melospiza melodia*) population on Mandarte Island, British Columbia, Canada. We believe much greater rates of nesting success are highly unlikely. We calibrated the parameters of Equation (3) with these assumptions and estimates to derive an estimate of nesting success response to edge for the Henslow's Sparrow population at Fort Knox (Fig. 6).

Results

Our habitat model predicted 859.5 ha of potential Henslow's Sparrow nesting habitat at Fort Knox (Table 5). The model aggregated this area into 3335 patches. However, only 21 (0.6%) of the patches were large enough to support nests (Table 6). The vast majority of the patches were too small for the establishment of territories. Either they were smaller than the territory size (88% of the patches were < 0.4 ha), or, because of the area sensitivity of Henslow's Sparrow (Fig. 1), the patches were unlikely to be occupied. The largest patch was only 51.1 ha. As a result, only 201.4 ha of the potential habitat was utilized.

The 21 utilized patches supported 100 nests and produced 440 eggs (Table 5), but only 33% of the nests successfully fledged young, so only 34% of the eggs were fledged. Four patches were responsible for 896. Productivity was limited to slightly less than 1.5 fledglings per pair, and only 49% (72) of the fledglings were female. Rarely, a patch produced only

Table 4. Life history parameters for Henslow's Sparrow used as model input.

Parameter	Value
Territory size (A_T)	0.4 ha
Gap crossing ability	< 20 m
Clutch size (C)	4–5 (uniform)
Incidence function parameters (β_0, β_1)	-2.55 0.97
Juvenile survivorship (s_0)	0.33
Subadult survivorship (s_1)	0.50
Adult survivorship (s)	0.57
Age of first reproduction (T)	1 yr
Maximum age of reproduction (L)	8 yr
Maximum nesting success ($S_{\max}$)	0.8
Edge:area index where $S_i = 0.5S_{\max}$	0.25
Shape parameter θ (Eq. 3)	0.5

male fledglings (i.e., patch 3161, Table 6). With $b = 0.720$ female fledglings per female, the expected net lifetime production of females per female (R_0) is < 1.0 (Table 7) (i.e., less than replacement), and the population's finite rate of increase (λ) is < 1.0 (Table 5). The landscape's production of females is insufficient to compensate for mortality reflected in juvenile and adult survivorship, and (in the absence of immigration and assuming constant demographic parameters) the population will decline at an annual rate of approximately 22% (Fig. 7).

The expected net lifetime maternity R_0 is a consequence of both survivorship and age-specific reproduction (Eq. 7). If more females live longer, lifetime maternity will increase even if age-specific reproduction remains low. Similarly, an increase in age-specific reproduction, perhaps through an increase in nesting success, can increase R_0 for a given survivorship. In Figures 8 and 9 we plot R_0 in the parameter space for maternity b and juvenile (s_0) and adult (s) survivorship, respectively. The shaded region in both Figures indicates the region of parameter space where $R_0 \geq 1.0$. In the shaded region the population will remain at a constant value or increase; elsewhere the population will decline. The filled circles in Figure 8 and 9 indicate the combinations of b and s_0 or s for Henslow's Sparrow at Fort Knox.

The combination of b and adult survivorship s at Fort Knox is sufficient to insure a steady state or increasing population (Fig. 9). Juvenile survivorship s_0 is, however, too low (Fig. 8). The model's prediction of a declining population at Fort Knox is a consequence of too little successful reproduction combined with too low a rate of juvenile survivorship.

Table 5. Model results for Henslow's Sparrow at Fort Knox.

Variable	Value
Total habitat	859.5 ha
Number of patches	3335
Number of patches utilized	21
Area of utilized patches	201.4 ha
Nesting density	0.12 pairs ha^{-1} of habitat
Total egg production	440
Total fledgling production	148
Nesting success	33%
Fledgling success	34%
Productivity (P_L)	1.480000
Female sex ratio	0.49
b	0.72
R_0	0.508
λ	0.778
Rate of change	-22.2% yr^{-1}

Table 6. Model patches large enough to support nests.

Patch number	Area (ha)	Edge:area index	Nests	Fledglings Total	Fledglings Female
167	5.1	0.39	1	0	0
252	5.0	0.42	1	0	0
691	4.2	0.49	1	4	2
734	4.3	0.29	1	0	0
796	4.8	0.36	1	4	2
817	4.5	0.30	1	0	0
838	42.8	0.22	29	53	30
923	4.0	0.34	1	0	0
1051	3.8	0.30	1	0	0
1717	3.6	0.38	1	0	0
1736	8.8	0.35	3	14	6
1865	51.1	0.30	37	42	18
1894	4.2	0.36	1	0	0
2574	3.8	0.39	1	5	2
2874	4.9	0.25	1	0	0
2918	3.5	0.22	1	0	0
2958	4.4	0.39	1	0	0
3155	20.5	0.30	11	22	12
3161	9.6	0.21	4	4	0
3291	3.7	0.27	1	0	0
3306	4.8	0.24	1	0	0

Table 7. Model generated life history table for Henslow's Sparrow at Fort Knox

x	l_x	m_x	$l_x m_x$
0	1.0	0.0	0.0
1	0.330	0.720	0.238
2	0.165	0.720	0.119
3	0.094	0.720	0.068
4	0.054	0.720	0.039
5	0.031	0.720	0.022
6	0.017	0.720	0.013
7	0.010	0.720	0.007
8	0.006	0.720	0.004
			$\sum l_x m_x = 0.508$

Discussion

Given the current landscape configuration at Fort Knox, our prediction of Henslow's Sparrow nesting habitat, and our estimates of Henslow's Sparrow life history parameters, the model indicates that the Fort Knox landscape is a population sink for Henslow's Sparrow. The combined values of reproductive output b and juvenile survivorship s_0 are substantially too low to support either a stable or increasing (i.e., source) population at Fort Knox (Fig. 8). Persistence of Henslow's Sparrow at Fort Knox requires recruitment of individuals from other parts of the species' range. This may represent the historical situation at Fort Knox, since the landscape is on the southern edge of the species' summer range, and may have always represented 'marginal' habitat. This hypothesis will require further testing with a map of Henslow's Sparrow nesting habitat thought to approximate potential, pre-European, or pre-agricultural vegetation. It would be premature to ascribe the model's assessment of the landscape as a sink for Henslow's Sparrow to military activity at Fort Knox. It is just as likely, if not more so, that agriculture outside the Fort Knox Reservation has substantially reduced and fragmented Henslow's Sparrow habitat in the region (see Fig. 4). But here again, it is premature to ascribe culpability.

Nevertheless, the model does suggest a focus for any management intervention to 'restore' the viability of the landscape for Henslow's Sparrow or to mitigate the apparent population sink, whatever its origin. Much of the annual mortality of juvenile Henslow's Sparrow likely occurs during migration to and from its wintering grounds in the grassland and pine-savannah ecosystems of the southern United States and on the wintering grounds themselves. There is obviously little a land manager in the summer breeding range of the species can do to

reduce this overwintering mortality. In any case, shifting the Fort Knox population from a sink to a steady state or source population through changes in juvenile survivorship alone, with no change in reproductive output, would require values of juvenile survivorship near 70% (Fig. 8). Values this high are probably unreasonable, and they would be very difficult if not impossible to achieve.

A land manager at Fort Knox, or elsewhere in the summer range of Henslow's Sparrow, is much more likely to influence the population dynamics of the species by increasing reproductive output (the maternity function b), primarily by manipulations of landscape structure and it's influence on nesting success. With juvenile survivorship at 0.33, an increase in b at Fort Knox from the current estimate of 0.72 to approximately 1.5 female fledglings per female would shift the population into the stable or increasing region of the parameter space for b and s_0 (Fig. 8). Assuming that 50% of the fledglings are female, and that the expected fledgling rate of successful nests is 4.5 fledglings per successful pair, a b of 1.5 would require a nesting success rate for the entire landscape of slightly less than 67%. That is approximately twice the current assessment's estimate of landscape-wide nesting success (33%, Table 5), but it is not an impossibly high value. Changes in the spatial configuration of the landscape that would favor higher nesting success (e.g., less edge) might also reduce the expectedly high mortality of fledglings on the breeding ground that occurs prior to their leaving for the winter. Any increase in juvenile survivorship reduces the increase in b needed to shift the population from sink to source (Fig. 8).

We have not pursued it here, but our model could be used to explore the influence of alternative spatial distributions and configurations of Henslow's Sparrow habitat on b and the

net lifetime maternity R_0. A spatial configuration with larger more contiguous patches with less edge per unit area would likely increase the expected occurrence of Henslow's Sparrow in larger patches and increase the landscape wide nesting success. This same conclusion might be reached, without the model, from general principles and expectations of small passerine response to habitat loss and fragmentation; it hardly justifies implementation of the model as an assessment tool. However, the model can do what the general principles cannot. It can provide quantitative estimates of the changes needed to achieve the desired goals—not only that a less fragmented landscape of larger more contiguous patches is desirable, but, how much reproductive output is required for a given estimate of survivorship, and which alternative spatial configurations (planned or proposed) are most likely to achieve that requirement.

Despite the relative simplicity of the model, it does involve a variety of assumptions, and some of the data inputs are highly uncertain, particularly those for the critical variables of nesting success and survivorship. Further development and application of the model as an assessment tool will require more substantial analysis of model sensitivity and uncertainty. The comparisons of b and survivorship in Figs. 8 and 9 provide some sense of the model's sensitivity and the importance of uncertainty in model inputs. For example, the prediction of a sink for Henslow's Sparrow at Fort Knox is unlikely to be simply a consequence of error or uncertainty in nesting success or juvenile survivorship. The change in either needed to alter the models assessment from sink to source is likely larger than even the considerable uncertainty in those model inputs (Fig. 8). Similarly, uncertainty in adult survivorship is unlikely to alter the models assessment of the Fort Knox landscape as a sink for Henslow's

Sparrow (Fig. 8). On the other hand, if we have overestimated nesting success in the less fragmented patches by assuming the high habitat quality associated with recently burned grasslands (see Fig. 6 and Johnson & Temple (1986)), then we could be overestimating b, and adult survivorship could be a more important parameter (Fig. 9). These results not withstanding, a more formal error and uncertainty analysis is called for, and the model should incorporate error and uncertainty propagation as an integrated part of its analysis and reporting of model results. The importance of error and uncertainty might not be so 'apparent' when the model is applied to other landscapes or other species, and the difference between a prediction of source or sink might be much more sensitive to model assumptions and data uncertainties.

Demographic models of the type we have presented here are a necessary part of assessing avian response to land use and habitat fragmentation. Population density can be a poor and misleading indicator of habitat and landscape quality (Van Horne 1983; Maurer 1986). Individuals may commonly exist and even breed in regular and substantial numbers in sink habitats, but they will not persist without immigration from source landscapes (Pulliam 1988; Howe et al. 1991; Pulliam & Danielson 1991). Source-sink demographics can interfere with the interpretation of even long-term census (density) data (Brawn & Robinson 1996). Variations in local abundance associated with source-sink dynamics can make the determination of long term trends for the species over its range very difficult, especially if those changes are slow. Sink landscapes may sometimes play an important and positive role in the demography of a metapopulation (or otherwise spatially structured population) with source and sink subpopulations (Howe et al. 1991), but the land managers response to an observed

decline in a natural sink landscape is likely to be different than to a similar observation in what had been identified as a source landscape. It is vital that assessments of land use and land-use change on avian populations include a quantitative analysis of demographic variables and trends (Van Horne 1983; Maurer 1986). Assessments of the presence of habitat or of density alone are not sufficient. Moreover, because landscape structure can influence key demographic variables, the assessment should include an explicit consideration of spatial pattern and changes in that pattern in response to land use change and land management. We have presented one model designed explicitly for that purpose. Others are available, for example the models of Urban et al. (1988) and Donovan et al. (1995), and models like them should be incorporated into the ecosystem management of public lands.

Concluding Remarks

We have shown that a relatively simple combination of landscape and demographic modeling can yield an effective assessment tool. It also provides a research tool for investigating the demographic consequences of landscape structure. Elsewhere, the model has been coupled with a neutral landscape model (Gardner et al. 1987) in a theoretical exploration of how changes in the proportion of available habitat shift a population from source to sink (King, unpublished). Feedback from theoretical investigations will improve the model in its more applied assessment applications.

Development and implementation of the model have also emphasized areas where additional empirical and theoretical investigation are needed. For example, models of nest occurrence as a function of patch size (the incidence functions) and estimates of minimum

area for breeding merit further attention. How consistent are these relationships from one location to another? How well does an incidence function for Henslow's Sparrow in Illinois (Herkert 1994) translate to a Henslow's Sparrow population in Kentucky or Kansas? Functional relationships between the probability of nesting success and a patch's edge:area ratio also need further development. The hypothesized relationship between edge:area ratio and nesting success we have developed here needs to be tested, for Henslow's Sparrow and Fort Knox in particular, but also to determine it's generality. Is knowledge of the edge:area ratio sufficient to predict nesting success, or is a more demanding knowledge of actual distance from edge required? Does the phenomenological representation of nest predation and brood parasitism we use here need to be replaced with more explicit mechanistic models of predation and parasitism?

Finally, the need for basic life history data cannot be underestimated, especially for species of conservation concern. In the absence of these data we are forced to extrapolate from other species in other regions that may be only weak ecological analogues. These data can be difficult to obtain (e.g., the low recapture rates of many long distance migrants makes estimating survivorship very difficult), and they can be empirically intensive, requiring long-term multi-year monitoring and many seasons of intensive field work. These data are crucial, however, for accurate and rigorous assessment of avian demographics and persistence in managed landscapes.

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Figure Captions

Figure 1. A sample of incidence functions for different bird species. The curve for Henslow's Sparrow is from Herkert (1994); the others are from Robbins et al. (1989).

Figure 2. The relationship between nesting success and the patch edge:area index. The curves indicate different types of possible response to increasing edge per unit area.

Figure 3. Location and detail of Fort Knox Military Reservation, Fort Knox, Kentucky.

Figure 4. Landcover map of Fort Knox, Kentucky. Landcover was determined by a supervised classification of LANDSAT Thematic Mapper (TM) imagery. See Hargrove et al. (submitted) for details.

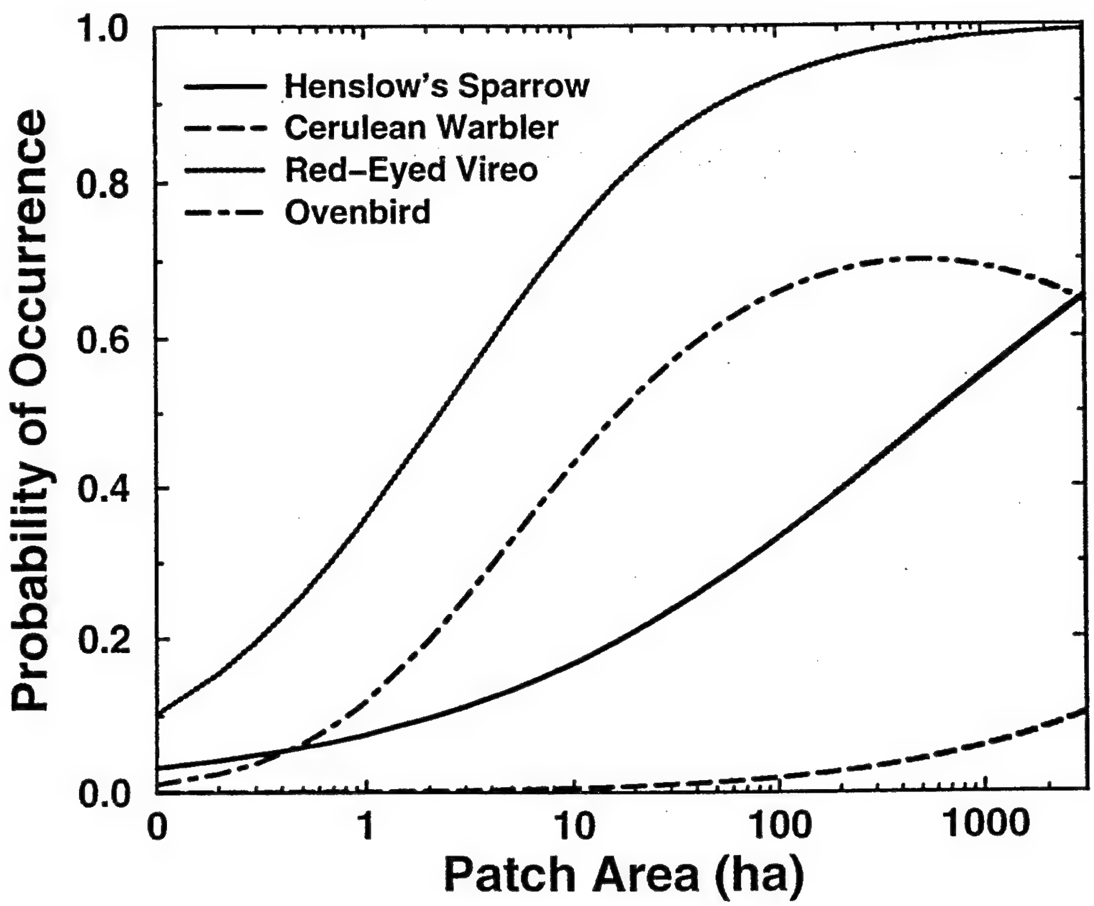
Figure 5. Predicted distribution of potential Henslow's Sparrow nesting habitat at Fort Knox, Kentucky.

Figure 6. An estimate of the relationship between nesting success and the patch edge:area index for Henslow's Sparrow at Fort Knox. The symbols are estimates derived from data in Johnson and Temple (1986) (see text). The solid curve is the fitted calibration of Equation 3 to the one year since burn points only, and is the relationship used in the model.

Figure 7. Model projection of the Henslow's Sparrow population at Fort Knox, Kentucky.

Figure 8. Net expected lifetime maternity R_0 as a function of age-specific maternity b and juvenile survivorship s_0. The shaded region indicates where $R_0 \geq 1.0$ and the population is at steady state or increasing. Outside this region the population $R_0 < 1.0$ and the population will decline. The filled circle indicates the combination of parameter values for Henslow's Sparrow at Fort Knox.

Figure 9. Net expected lifetime maternity R_0 as a function of age-specific maternity b and adult survivorship s. The shaded region indicates where $R_0 \geq 1.0$ and the population is at steady state or increasing. Outside this region the population $R_0 < 1.0$ and the population will decline. The filled circle indicates the combination of parameter values for Henslow's Sparrow at Fort Knox.



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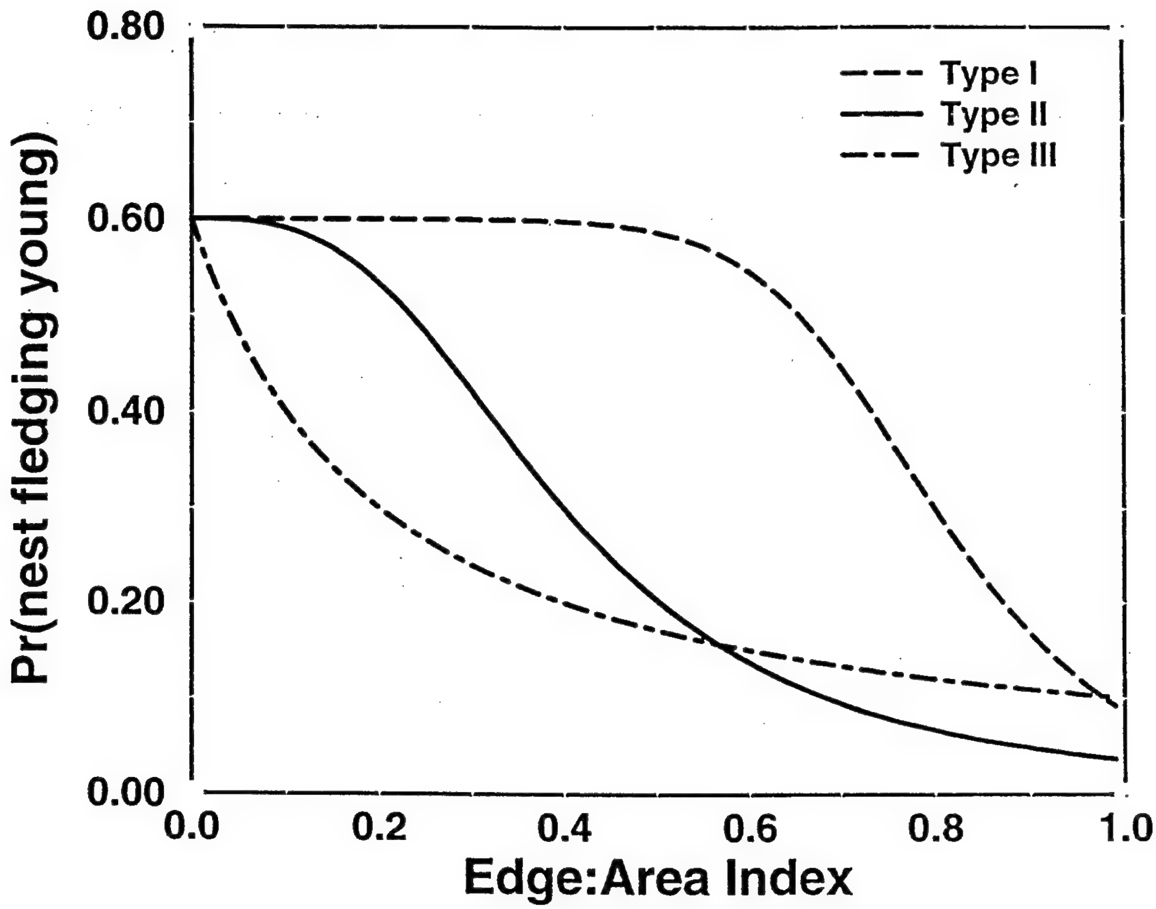

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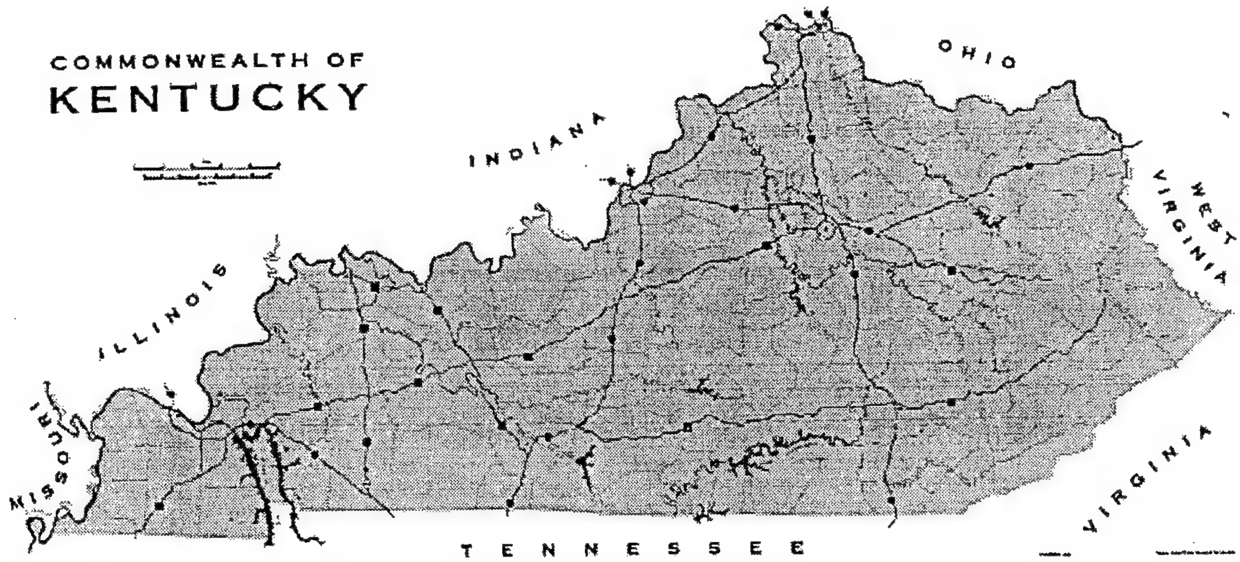

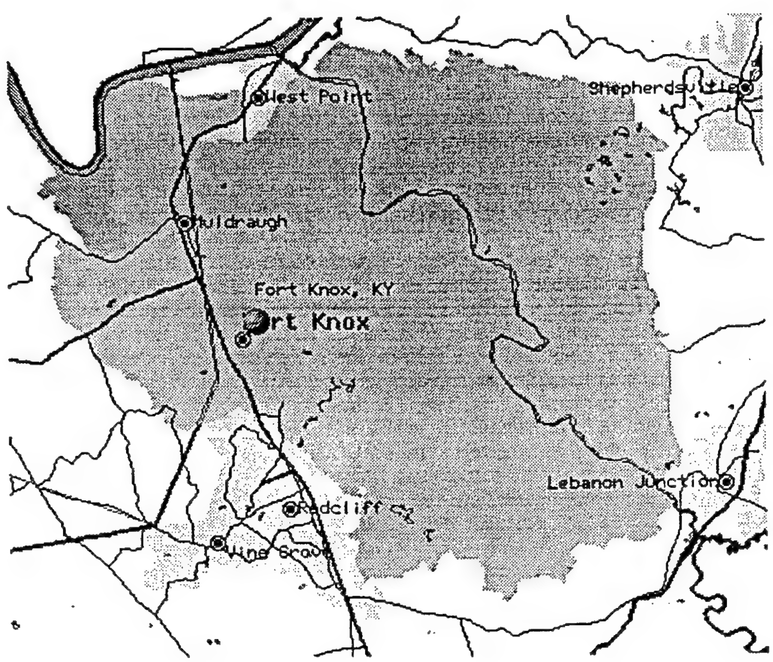

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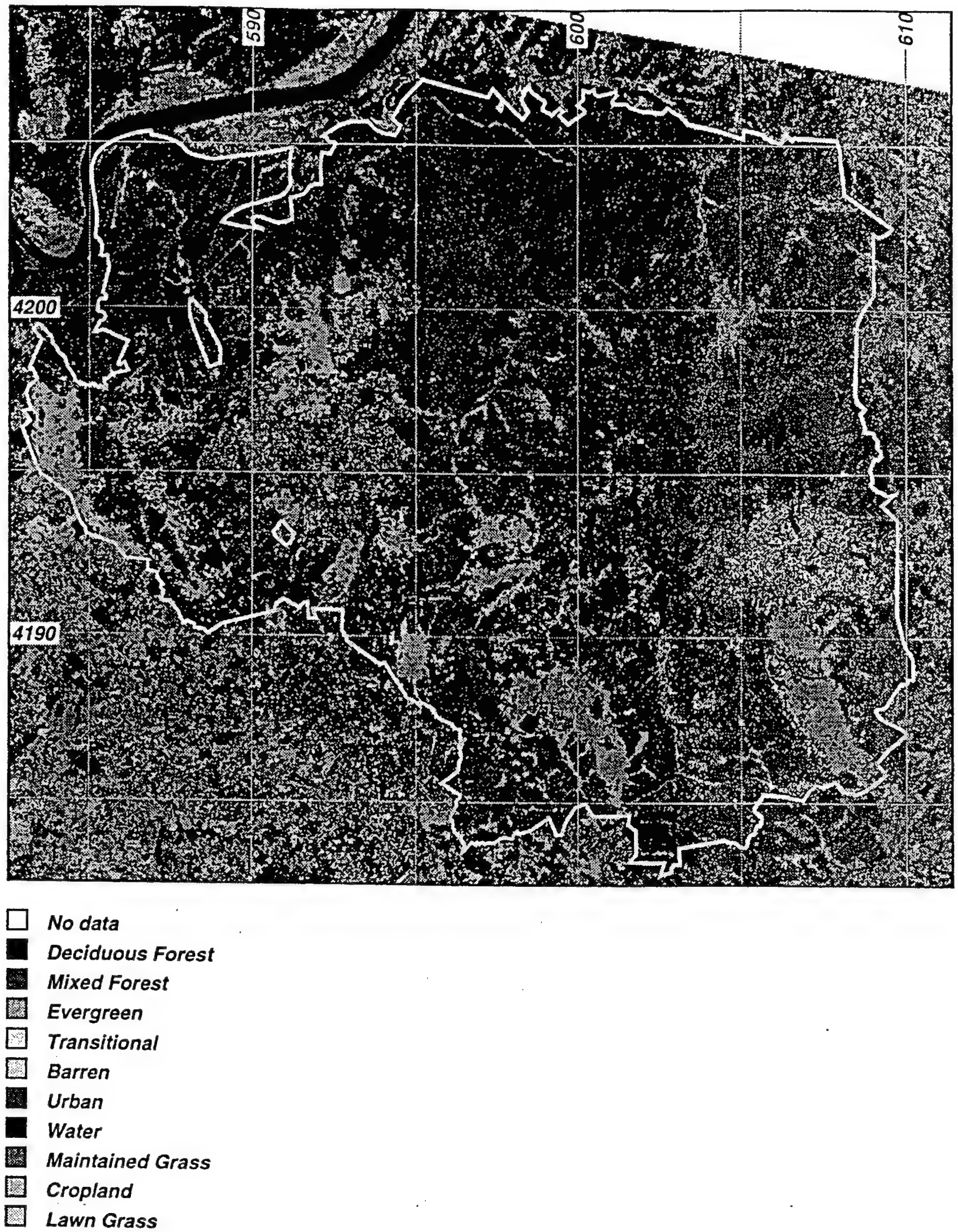

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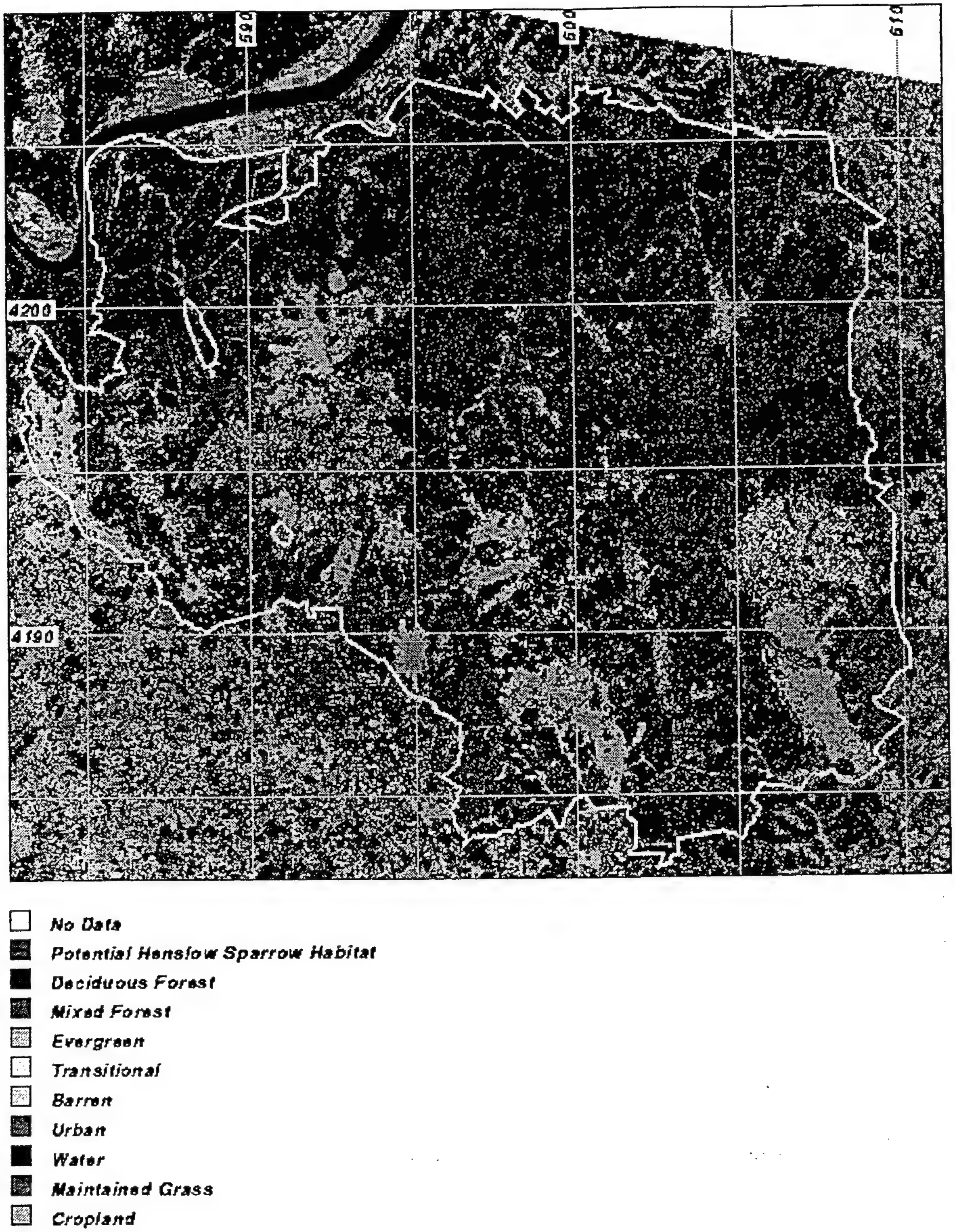

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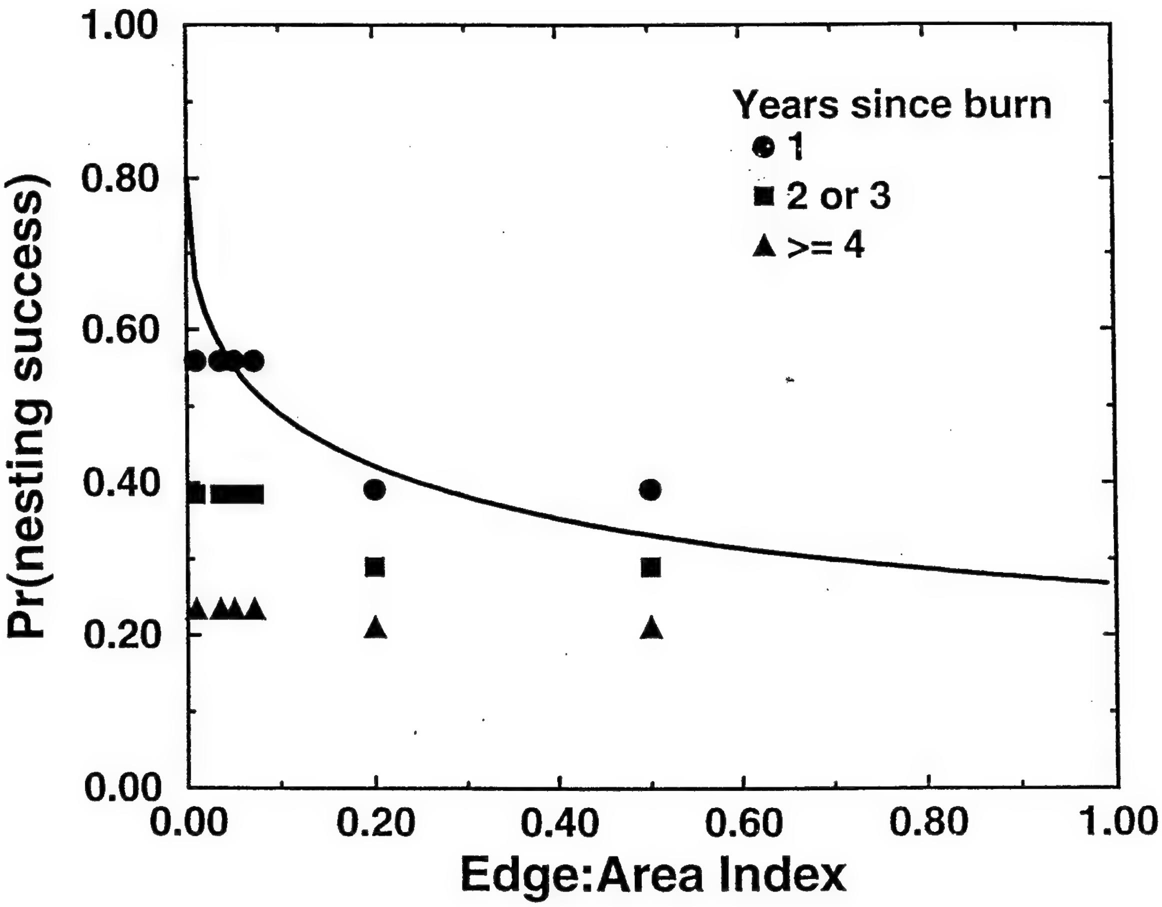

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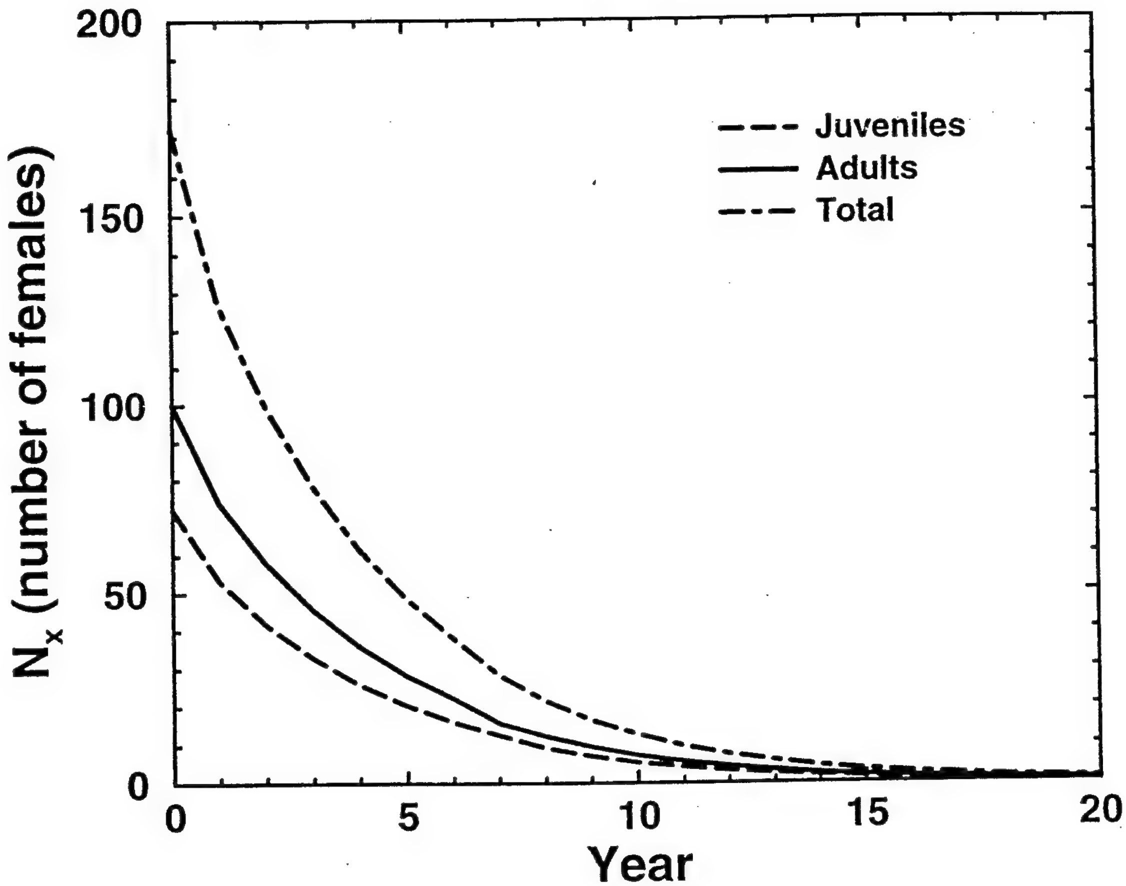

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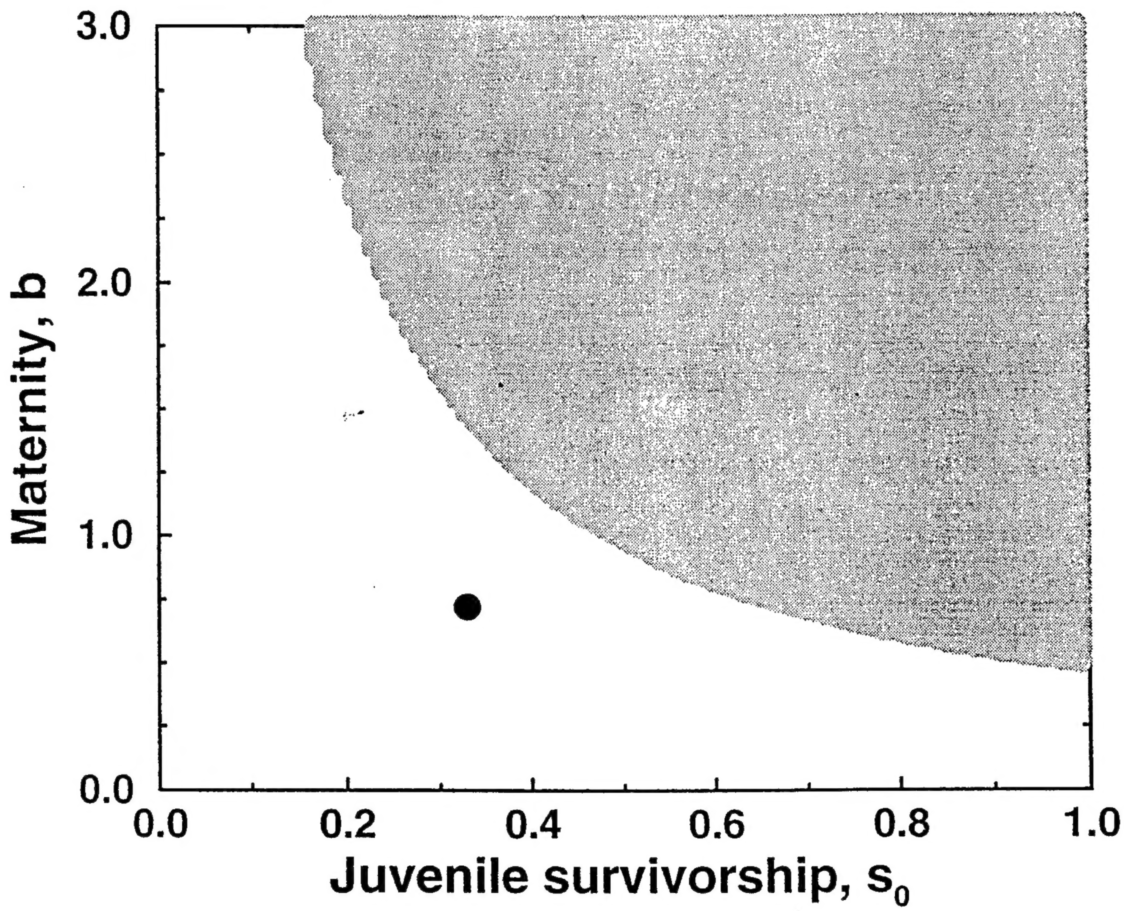

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Ashwood T. L., V. H. Dale, W. W. Hargrove, A. W. King, And L. K. Mann. GIS-Based Habitat Modeling at Fort Knox. SERDP Symposium, November 20–22, 1996, Tyson's Corner, VA.

Military lands frequently contain important biological resources such as rare plants and animals and ecologically important habitat types. In order to provide appropriate stewardship of these resources, while still maintaining or expanding traditional military activities (e.g., training), land managers must have reliable information on the location of the resources. Traditionally, this information has been obtained through exhaustive field studies that are expensive and time consuming and are not readily amenable to frequent updates. We present a series of habitat models utilizing readily available data in a Geographic Information System. These models can be developed with a minimum of field work from existing information. Moreover, as changes occur (i.e., land use changes) or as other resource concerns are identified, the models can be quickly updated.

Most habitat models utilize only land use/land cover data. Such models may seriously overpredict or underpredict the presence of habitats of concern. Our approach combines other broad spatial data layers, such as soil type and underlying geology, with land use/land cover and inductive models based on known locations. We present habitat models for Henslow's sparrow, cerulean warbler, and cedar barrens. The models were developed and tested at Fort Knox (KY), but the concepts are readily transferable to other sites and to other species or habitat types.

Ashwood, T. L., W. W. Hargrove, A. W. King, L. K. Mann, V. H. Dale and L. G. Pollock. Using LCTA Data To Build GIS-Based Habitat Models At Fort Knox. Sixth Annual ITAM Workshop, August 25–28, 1987, San Antonio, TX.

Military lands frequently contain important biological resources such as rare plants and animals and ecologically important habitat types. In order to provide appropriate stewardship of these resources, while still maintaining or expanding training activities, land managers must have reliable information on the location of the resources. Traditionally, this information has been obtained through exhaustive field studies that are expensive and time consuming and are not amenable to frequent updates. We present habitat models based on LCTA and other readily available data in a Geographic Information System. These models can be developed with a minimum of field work. As changes occur (i.e., land use changes), or as other resource concerns are identified, the models can be quickly updated.

Habitat models that utilize only land use/land cover data may seriously overpredict or underpredict the presence of habitats of concern. Our approach combines other broad spatial data layers, such as soil type and underlying geology, with LCTA-derived land use/land cover and inductive models based on known locations. Models for Henslow's sparrow, Cerulean warbler, and cedar barrens were developed and tested at Fort Knox (KY), but the concepts are readily transferable to other sites and to other species or habitat types. We also developed a

model of suitable "habitat" for tank training, which can be used to predict potential conflicts between training and other resources.

King, A. W., T. L. Ashwood, V. H. Dale, and L. K. Mann. Habitat Fragmentation and Regional Persistence of the Red-Cockaded Woodpecker. 12th Annual Landscape Ecology Symposium, March 16–19, 1997, Durham, NC.

Fire management, deforestation, forestry practice, and other changes in land use have reduced and fragmented the once extensive pine savannah ecosystems of the southeastern United States. The distribution of longleaf pine (Pinus palustris) alone has been reduced from perhaps 37 million hectares prior to European settlement to currently less than 1.2 million hectares. This large-scale alteration of the regional landscape has had consequences for many species, including the endangered red-cockaded woodpecker (RCW; Picoides borealis). Endemic to mature pine forests of the Southern U.S., remaining populations of the once abundant and widespread RCW are fragmented, small, and isolated. Along with absolute habitat loss, fragmentation of the landscape may have contributed to the decline of RCW. We employ a series of spatially implicit and explicit metapopulation models to assess the regional persistence of the RCW. We use these models to address two questions: (1) is the current spatial distribution of RCW habitat consistent with long-term persistence of the regional metapopulation, and (2), if not, what changes in habitat distribution or other management interventions may be required to promote regional persistence. We discuss our results within the larger context of regional landscape management for the conservation of regional populations.

King, A. W., T. L. Ashwood, V. H. Dale, and L. K. Mann. On the Persistence of the Red-Cockaded Woodpecker, *Picoides borealis*, in the Southeastern United States. 58th Annual Meeting of the Association of Southeastern Biologists, April 16–19, 1997, Greenville, SC.

The red-cockaded woodpecker (RCW; Picoides borealis) is an endangered species endemic to mature pine forests of the southeastern United States. Fire management, deforestation, forestry practice, and other changes in land use have reduced and fragmented the once extensive pine savannah habitat preferred by RCW. Remaining populations of RCW are small, isolated, and fragmented. Isolation and fragmentation may have negatively impacted juvenile dispersal and contributed to the species' decline throughout the Southeast. We use a series of metapopulation models to address this question and to assess the regional persistence of RCW. We address two questions: (1) is the current distribution of RCW habitat across the Southeast consistent with long-term persistence of the regional metapopulation, and (2), if not, what changes in habitat distribution or other management interventions (e.g., translocation to subsidize interpopulation dispersal) are needed to ensure regional persistence.

King, Anthony W., Linda K. Mann, William W. Hargrove, Tom. L. Ashwood, and Virginia H. Dale. A Model of Spatially Structured Avian Demographics. Annual Meeting of the International Society for Ecological Modeling, August 4–6, 1997, Montreal, Quebec, Canada.

We describe a model of how the spatial distribution of nesting habitat affects the reproductive success of territorial migrant bird species breeding in fragmented landscapes. The model combines a landscape perspective with conventional avian demographic modeling to provide a tool for the assessment of how land-use change might impact the persistence of avian populations. Nesting habitat is mapped with a regular grid of square cells. Neighboring cells are aggregated to form patches. Territories are distributed among patches using logistic regressions describing the relationship between species' occurrence and patch area. Nesting success in each patch is a function of the patch's edge:area ratio, reflecting the association of edge with increased risk of predation and brood parasitism. The number of female fledglings produced by all patches is used to calculate the expected number of female fledglings per female. This demographic variable, an explicit consequence of landscape structure, is combined with survivorship in a life-table model to calculate the demographic indices of net lifetime maternity and the finite rate of increase. These indices provide a simple characterization of the landscape as a population source or sink. We describe an implementation of the model for Henslow's Sparrow (Ammodramus henslowii) at the Fort Knox Military Reservation, Fort Knox, Kentucky. The model indicates that the Fort Knox landscape is a population sink for Henslow's Sparrow, with an annual rate of decline of approximately 22%. Analysis of the model results suggest that the prediction of a declining population at Fort Knox is a consequence of too little successful reproduction combined with too low a rate of juvenile survivorship.

Mann, L. K.*, R. Washington-Allen, W. Hargrove, T. Ashwood, V. Dale, A. King, and R. McCord. Predictive Modeling of Eastern Limestone Barrens in Heterogeneous Landscapes Using Multiple Geographic Information System Data Layers. Ecological Society of America Meeting, August 10-14, 1997, Albuquerque, NM.

Military lands frequently contain important biological resources and ecologically important habitat types. Stewardship of these resources is enhanced by predicting their spatial distribution. Geographic Information Systems have potential to accurately predict locations of these resources in complex or inaccessible terrain from existing data with a minimum of field work. The limestone barrens at the Department of Defense Fort Knox Military Reservation and the Department of Energy Oak Ridge Reservation (DOE-ORR) are of conservation interest because of 1) their rarity as a community, 2) their importance as habitat for several globally rare plant species, and 3) their potential to provide habitat for rare invertebrates and other wildlife. Using edaphic requirements of vegetation and GIS data layers of soils, geology, slope, and landcover, we developed habitat models which predict the occurrence of limestone barren habitat at the DOE-ORR. At Fort Knox, field validation and comparison to maps of known cedar barrens demonstrated that the model was greater than 90% accurate in predicting locations of limestone barrens.